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TWO NEW GENERA OF MARINE ISOPOD CRUSTACEANS (CIROLANIDAE) FROM MADANG, PAPUA NEW GUINEA

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Aatolana gen.nov. is characterized by lobate pleopod peduncles, medially indented cephalon anterior margin, and posteriorly acute epimera on pleonite 3. *Aatolana rapax* sp.nov., the type species, is described from specimens trapped at depths from 150-450m off the outer reef slope at Madang. *Aatolana schiodtei* comb.nov. is transferred from the genus *Cirolana*. *Plakolana* gen.nov. is characterised by flattened posterior pereopods provided with long setae and spines, a medially indented cephalon anterior margin, elongate frontal lamina, quadrate pleopod 1 peduncle and the unique shape of the epimera of pleonite 3. *Plakolana accola* sp.nov., the type species, is described from trapped specimens off the outer reef slope at Madang, at depths from 300 to 450m. *Plakolana nagada* sp.nov. occurs within the barrier reef in shallow (16-22m) silty or sandy bottoms. *Plakolana* sp. and *P. binyana* comb.nov. are transferred from *Cirolana*. Both genera are known only from the Southwest Pacific. □ *Isopoda, Cirolanidae, new genera, new species, Aatolana, Plakolana, southwest Pacific, taxonomy.*

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Published reports devoted to the marine isopod fauna of New Guinea are few (see Bruce, 1982, Jones et al., 1983) although a number of records have recently been published as part of longer reports (e.g. Bruce, 1986a,b; Bruce & Harrison-Nelson, 1988; Williams & Williams, 1992). The nearby region of tropical and subtropical Queensland has received more attention from isopod taxonomists, and there the family Cirolanidae is represented by 52 species in 12 genera (although numerous species still remain to be described).

In 1989, I spent three weeks at the Christensen Research Institute at Jais Aben, Madang surveying the isopod fauna of the reefs and, to a lesser extent, near-reef sediments, from the intertidal to a depth of about 30m. Cirolanids were sampled at greater depths by the use of baited traps. The area proved to have a rich and diverse isopod fauna with well in excess of 100 species. With more thorough sampling of particulate sedimentary habitats this total should rise even further.

The family Cirolanidae is represented in the Madang collection by about 27 species in 11 genera, indicating a very high diversity when compared to figures available for single localities elsewhere. For example, Heron Island, a well collected location at the southern end of the Great Barrier Reef has 16 species in 7 genera (Bruce, 1986a). The entire Caribbean region has a total 22 free-living species (Kensley & Schotte, 1989),

while Aldabra Island, in the Western Indian Ocean, when surveyed by Kensley (1988), yielded only 3 species.

MATERIAL AND METHODS

Specimens were collected using methods described in Bruce (1986). Appendages were dissected from the right side of the specimen unless stated otherwise in the figure captions. All species described here were collected by setting baited traps overnight. The trap design is a 'minnow trap' made of storm drain piping fitted with end caps to which cut off funnels had been fitted.

Drawings of appendages were made using a compound microscope for *Plakolana* and a dissecting microscope for the larger *Aatolana*.

Pereopod orientation is identified as anterior (= superior) and posterior (= inferior); the margin to which the dactylus folds is regarded as posterior in both pereopods 1-3 and 4-7, even though the orientation of the posterior limbs is reversed; the lateral surface is the outward facing surface of the pereopod, and mesial is inward facing. Anterior (An) and posterior (Po) are identified on Fig 2.

Specimens have been deposited at the Queensland Museum (QM), Australian Museum (AM) and Museum of Victoria (NMV). Voucher samples have been donated to the San Diego Natural

History Museum. PMS= plumose marginal setae; BL= body length.

TAXONOMY

GENERAL REMARKS

Bruce (1986a: 223) listed a number of cirolanid species as incertae sedis, all but one being retained in *Cirolana*. Since that time only one, *Protognathia bathypelagica* (Schultz, 1977) has been relocated (Wägele & Brandt, 1988). Two of the species described by Bruce (1986a), *Cirolana schiodeli* Miers and *Cirolana* sp., were regarded as not conforming to the concept and diagnosis of *Cirolana*, but establishment of new monotypic genera was regarded as premature. Bruce (1991) later described a species that was obviously very similar to *Cirolana* sp. of Bruce (1986a) with the same set of characters that precluded assignment to *Cirolana*. That species was placed in *Cirolana*, also with the caveat of incerta sedis. The discovery of the species described here now provides a solid foundation to establish new genera for these species. In so doing, the generic concept of *Cirolana* can also be refined. It can now be stated that in *Cirolana* (sensu stricto) the anterior margin of the cephalon is with a rostral point or smoothly rounded (never medially indented); pleonite 3 does not encompass pleonites 4 and 5, though pleonite 3 is often posteriorly produced; pleonite 3 (in all Australian species) is narrowly rounded or acute; pereopods 5-7 are without long setae or long spines, and are robust (i.e. have few short spines, and no flattened articles).

Aatolana gen. nov.

Body without tubercles or dorsal sculpture. Cephalon without rostral point, anterior margin medially indented. Eyes large, about 3 times as long as wide. Pereonite 1 about twice as long as pereonite 2. Pleon with 5 visible segments; pleonite 3 with epimera expanded, posteriorly acute, extending to or beyond pleonite 5. Pleotelson with stout spines and PMS.

Antennule peduncle articles of about equal length; article 2 shortest. Antennal peduncle with articles 1-3 short, 4 and 5 longest. Frontal lamina slightly longer than wide; anterior margin curved, visible in dorsal view, with dorsally deflected apical point. Mandible with spine row and molar process well developed; lacinia mobilis absent;

incisors asymmetrical, right with 3 prominent cusps, left with middle cusp reduced. Maxillule with stout spines on lateral lobe; 3 robust circumplumose spines on medial lobe. Maxilla with all lobes well developed. Maxilliped palp with lateral and medial margin setose; endite with 2 coupling hooks.

Pereopods 1-3 with anterodistal margins of ischium and carpus not produced; posterior margin without elongate spines. Pereopods 5-7 subsimilar. Pereopod 7 with all articles robust, not flattened or natatory; basis with row of setae on posterior margin and lateral carina. Pereopod dactylus without distinct secondary unguis. Penes present on sternite 7, flattened, rectilinear, about twice as long as wide.

Pleopod 1 exopod lateral margin convex, apex narrow. Pleopods 1-3 with both rami with PMS; pleopods 3 and 4 endopods with reduced PMS; endopod of pleopod 5 without PMS. Peduncles of pleopods 1-5 with lateral margin forming, complex refolded lobe. Pleopod 2 appendix masculina basally attached, elongate, longer than endopod. Pleopod 1-4 exopods with slender accessory lamella at posterior proximolateral angle. Uropods with stout spines; mediolateral angle of peduncle produced.

Female: Maxilliped with lamina vibrans in ovigerous specimens. Brood pouch composed of oostegites arising from coxae 1-5. Pleopods 2-5 with accessory lamellae more prominent than in male.

TYPE SPECIES

Aatolana rapax sp. nov., here designated.

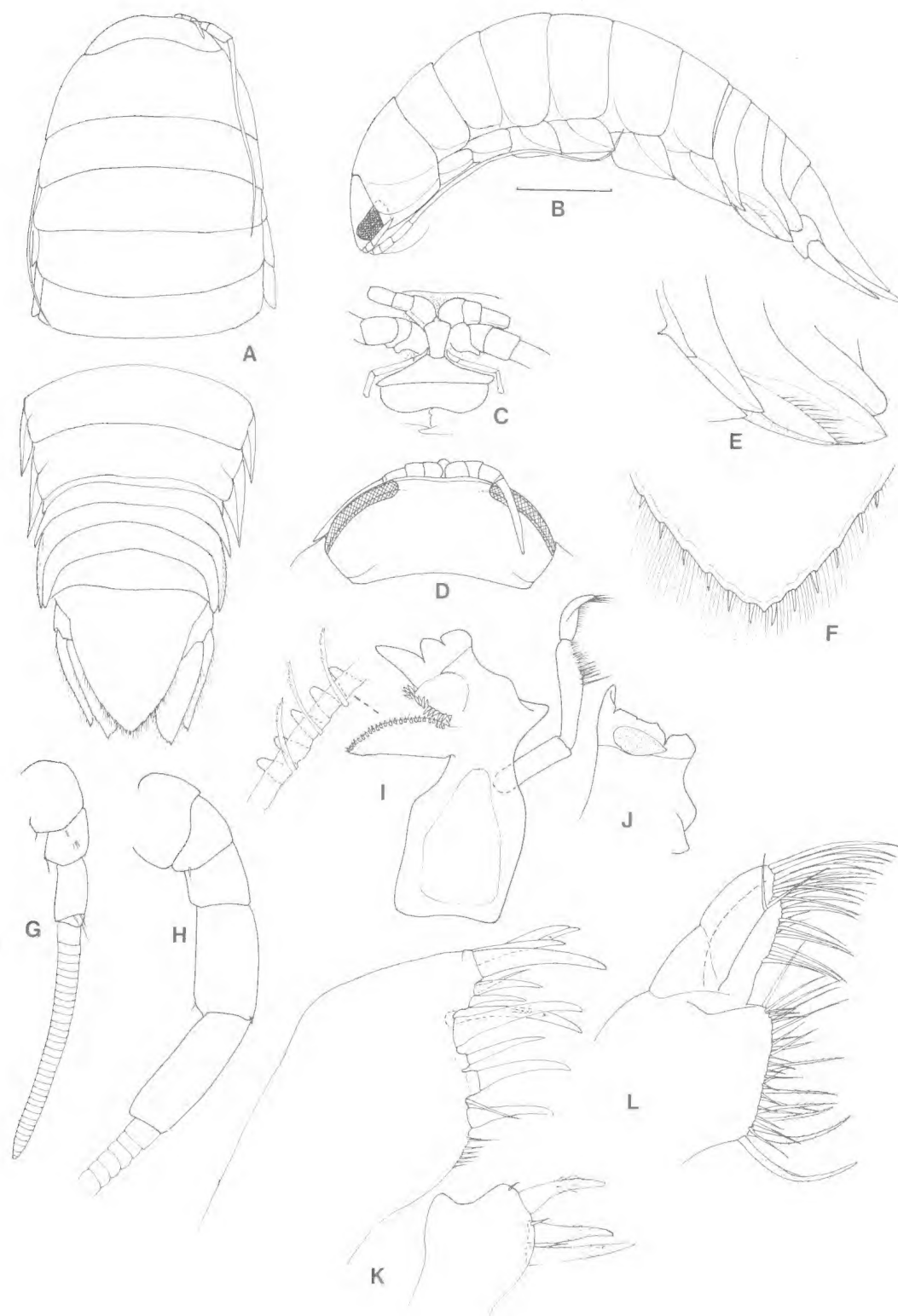
ETYMOLOGY

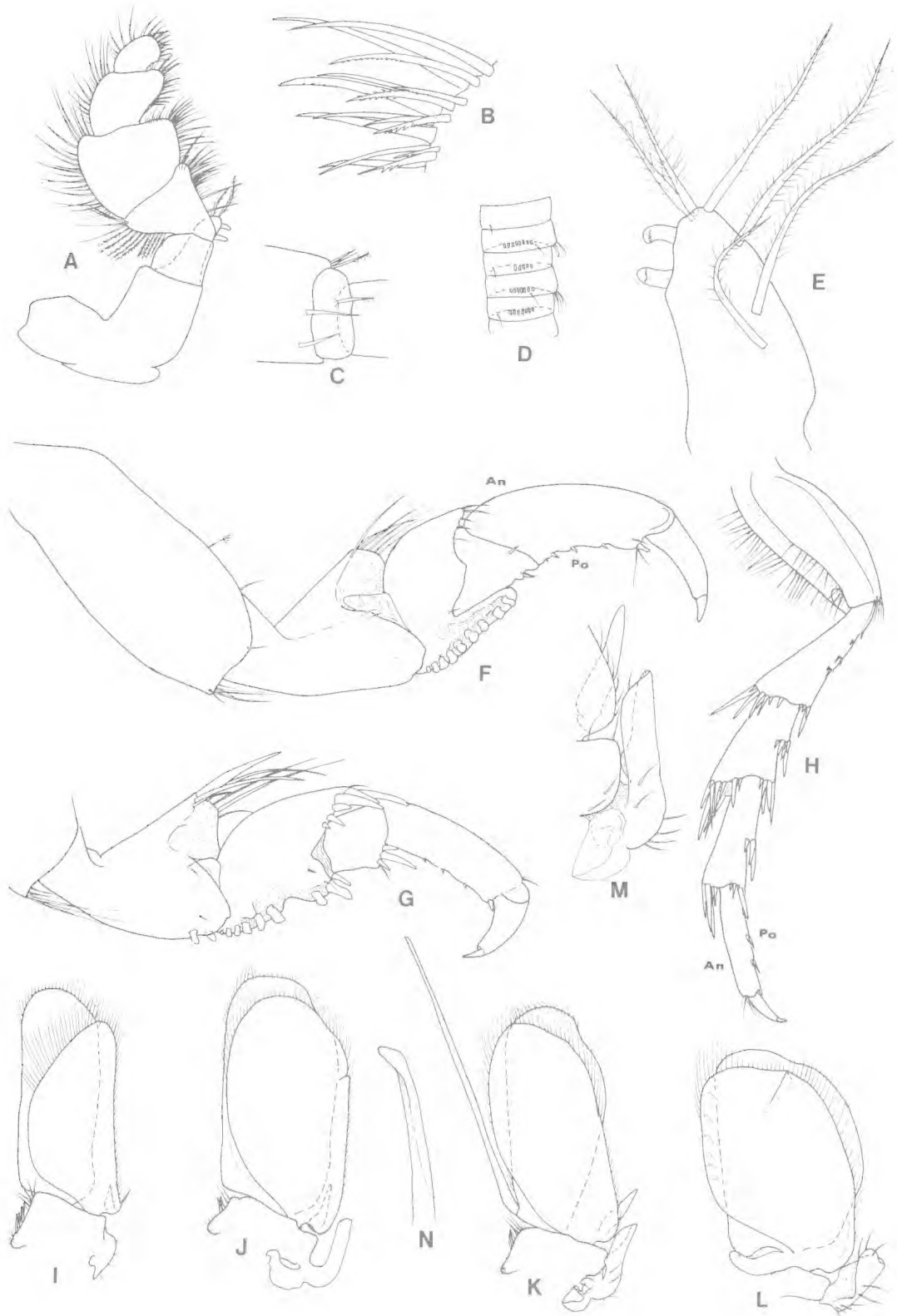
From the Greek *Aatos* (insatiable, referring to the ability of this species to devour fish carcasses) combined with *-lana*. Gender is feminine.

REMARKS

Characters by which this genus can be identified are the unique apomorphies of the pleopod peduncle lobes and the frontal lamina structure, and also the prominent and posteriorly acute epimera on pleonite 3. Other characters which also identify the genus, though not unique, are the medially indented anterior margin of the cephalon, the shape of pleopod 1 exopod, and the prominent flattened penes. The medially indented anterior margin of the cephalon is a subtle char-

FIG. 1. *Aatolana rapax* sp. nov. A-F holotype, remainder ♂ paratype 32.3mm. A, dorsal view; B, lateral view; C, frons; D, cephalon, dorsal view; E, pleonites, lateral view; F, telson apex; G, antennule; H, antenna peduncle; I, right mandible; J, left mandible incisor; K, maxillule; L, maxilla. Scale represents 4.0mm.





acter, but is none the less clearly expressed by those genera that show it.

The genus *Cirolana* has no species with medially indented cephalon, flattened rectilinear penes, lobate pleopod peduncles or large epimera on pleonite 3. Additionally *Cirolana* species all have a prominent secondary unguis on the pereopod dactylus and more plumose marginal setae on the endopods of pleopods 3 and 4.

OTHER SPECIES

Aatolana schioedtei (Miers, 1884) comb.nov. Tropical Australia, from Rottnest Island, Western Australia to Hayman Island (Bruce, 1986a).

AFFINITIES

Aatolana is similar only to *Booralana* Bruce, 1986. Both genera share similar-shaped pleopod rami, have similar elongate eyes, prominent flattened penes, medially indented cephalon and prominent epimera on pleonite 3. The frontal lamina structure of the two genera differ, and in *Booralana* pleonite 2 has well developed epimera, pleonites 2 and 3 both having a ventral flange. Additionally in *Booralana* the pleotelson and uropods are without spines.

KEY TO THE SPECIES OF AATOLANA

1. Pleonite 4 posterolateral margin rounded; uropod endopod lateral margin straight; pleotelson dorsal surface never setose
..... *A. rapax*
- Pleonite 4 posterolateral margin acute; uropod endopod lateral margin sinuate; pleotelson dorsal surface of large males setose
..... *A. schioedtei*

Aatolana rapax sp.nov. (Figs 1-3)

MATERIAL EXAMINED

HOLOTYPE: ♂ (28.7mm), outer reef slope, 5°8.4'S, 145°49.0'E, 3 May 1989, 200-150m depth, baited trap, coll. N.L. Bruce & M. Jebb (QM W17467).

PARATYPES: 9♂♂ (20.0-32.2mm, m=28.3), 4 ovig ♀♀ (29-33mm, mean 30.5), 6 non ovig ♀♀ (21-31mm, mean 24.7); 2 manca (7.0, 7.7mm), subsampled from c.200 specimens, data as for holotype (QM W17468).

OTHER MATERIAL: 200 specimens, topotypic series, same station as holotype, (QM W17471, NMV J27477, San Diego Natural History Museum). 4♂♂, 38♀♀, as for holotype, but 28 Apr 1989, 450m (QM W17469). 200+ specimens, as for holotype, but 29 Apr 1989, 300m (QM W17470). 93 specimens (mostly immature) outer barrier reef, between Rasch Pass and Wongat Is., 5°8.7'S, 145°49.7'E, 26-27 Jan 1990, 240m depth, coll. J.K. Lowry, J. Mizeu, J.D. Thomas (AM P40160).

DESCRIPTION

Body about 2.6 times as long as wide; pereonite 1>2=3<4=5<6>7. Pleonite 1 largely concealed by pereonite 7, epimera of pleonite 3 with posterior margin acute, with 3 longitudinal carina, medial one of which is provided with long setae; posterior margins of pleonite 4 epimera rounded, with very weak longitudinal carina. Pleotelson with lateral margins convex, converging to acute apex either side of which are 6 stout spines set amongst single row of PMS; spines restricted to distal third of pleotelson; proximal half (0.48) of lateral margin without PMS.

Cephalon with anterior submarginal furrow, dorsal interocular furrow running along top of eyes, but not extending beyond eyes. Antennule peduncle article 1 longest, 2 shortest; 4th short terminal article present; flagellum composed of about 32 articles, 1.5 times as long as peduncle, extending to anterior of pereonite 1. Antenna flagellum with about 60 articles, extending to anterior of pereonite 6. Frontal lamina as for genus. Mandible spine row with 19 spines; molar process with 27 spines interspersed with stout serrate setae; palp article 2 longest, with dense setose fringe on outer distal margin; article 3 lateral margin with continuous setae. Maxilla with 10 and 13 setae on lateral and middle lobes respectively; medial lobe with 1 large and 4 smaller circumplumose setae; anterior to these are two ranks of setae, posterior rank of 13 simple setae, anterior rank of 8, distal 5 of which are long. Maxilliped palp with simple setae on lateral margins of articles 3-5, PMS on article 2; articles 2-5 with about 15, 35, 20 and 11 lateral setae respectively; medial margins of articles 2-5 with about 19, 20, 12 and 12 setae respectively; article 5 with some serrate setae; endite with 6 long plumose setae.

FIG. 2. *Aatolana rapax* sp.nov. All figs of ♂ paratype 32.2mm, except N. A, maxilliped; B, distal margin, maxilliped palp article 5; C, distal margin, antennule peduncle; D, antennal flagellum, articles 23-27; E, maxilliped endite; F, pereopod 1; G, pereopod 2; H, pereopod 7; I-L, pleopods 1,3,2,5 respectively; M, pleopod 2 peduncle lateral margin; N, apex of appendix masculina, ♂ 31.5mm (An = anterior margin, Po = posterior margin).

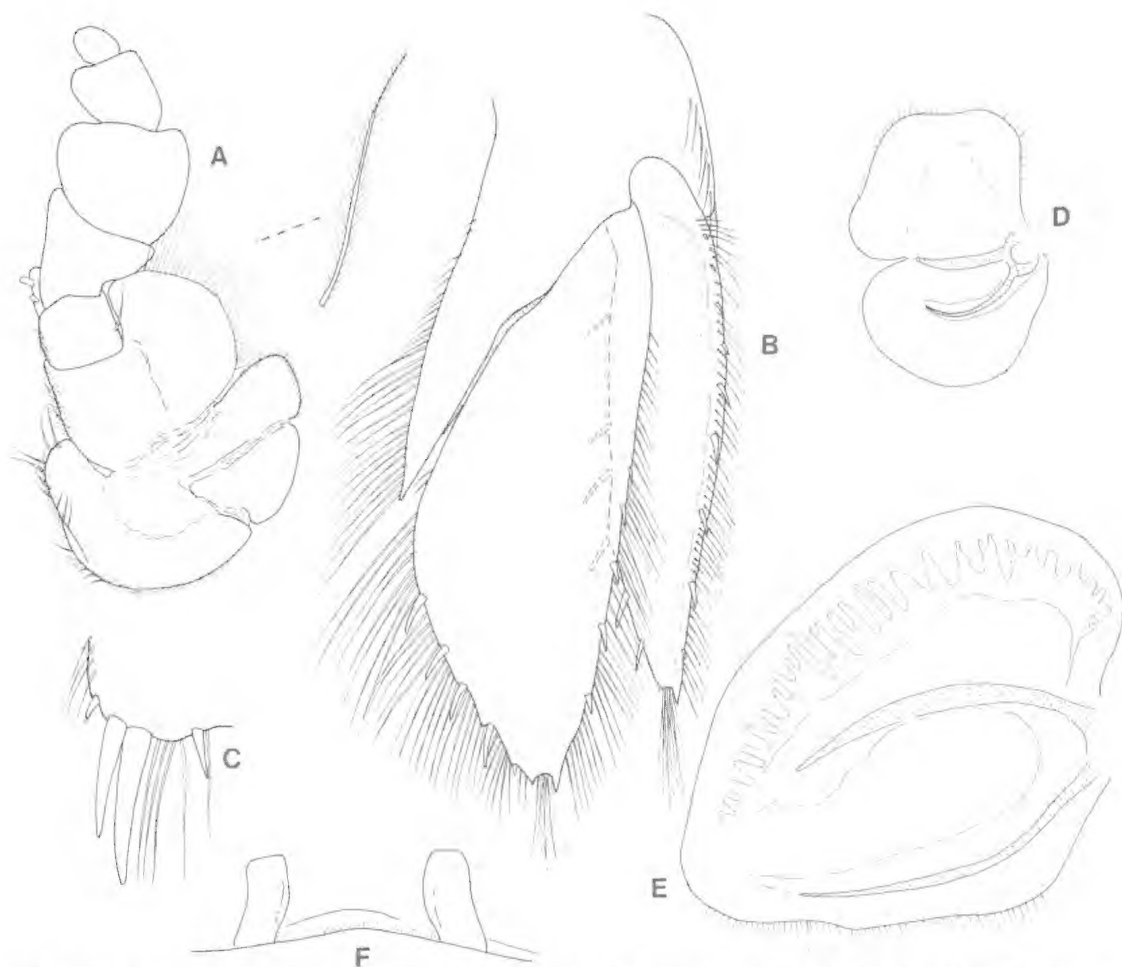
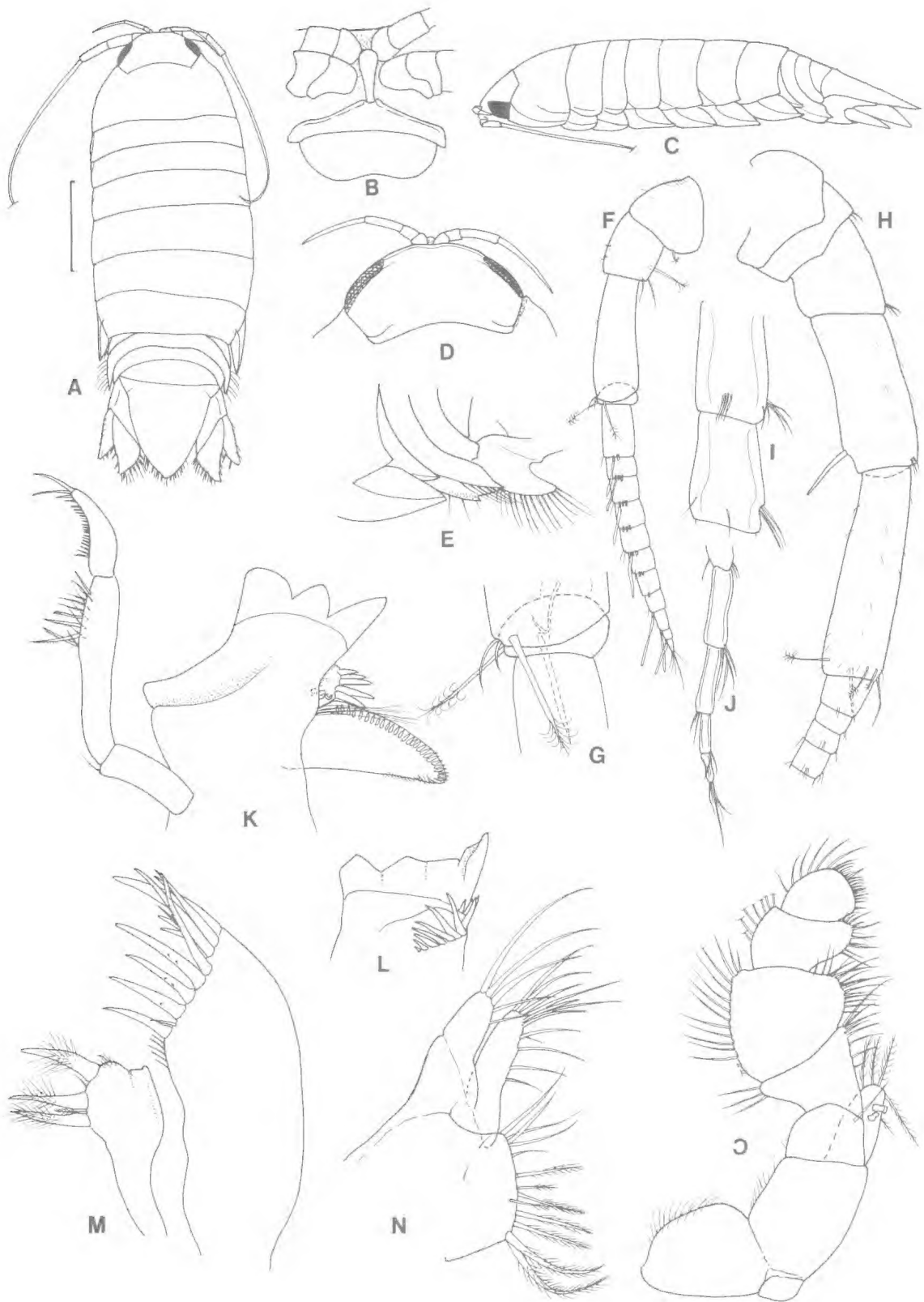


FIG. 3. *Aatolana rapax* sp. nov. A, D, E, ovig. ♀ paratype 29.4mm. A, maxilliped, showing lobes; D, oostegite 1; E, oostegite 5; B, uropod, ♂ paratype 32.2mm; C, ventrolateral angle, uropod peduncle, ♂ 32.2mm; F, penes, *in situ*, holotype.

Pereopod 1 basis with 5 setae at posterodistal angle; ischium with 6 setae at anterodistal angle; merus with 9 tubercular spines on posterior margin, 5 short simple setae at anterodistal angle; carpus with single spine on posterior margin; propodus with 3 spines on palm, 4th larger spine opposite base of dactylus. Pereopod 2 longer than 1; ischium with 6 long spines anterodistal angle, 2 robust spines posterodistal angle; merus with indented posterior margin, proximal portion with 6 stout spines, anterior portion with 2 large stout and 1 acute spine and 6 stout spines at anterodistal

angle; carpus with 4 spines at anterodistal angle; propodus with 3 small spines, 4 spine at anterodistal angle; propodus with 3 small spines, 4th spine opposite base of dactylus. Pereopod 7 basis with fringe of setae on anterior margin and median carina; posterior margin of ischium with 3 clusters of short setae, 4 large spines at posterodistal angle; merus and carpus with cluster of spines on posterior margin and posterodistal angle; ischium-carpus with clusters of spines at anterodistal angles only; propodus with 3 pairs of spines on posterior margin.

FIG. 4. *Plakolana accola* sp. nov. A-E, holotype, ♂ remainder paratype 9.3mm. A, dorsal view; B, frons; C, lateral view; D, cephalon; E, pleonites, lateral view; F, antennule; G, distal margin, antennule peduncle; H, antennal peduncle; I, antenna, flagellum articles 9 and 10; J, antenna, flagellum terminal articles; K, right mandible; L, left mandible, incisor and spine row; M, maxillule; N, maxilla; O, maxilliped. Scale represents 2.0mm.



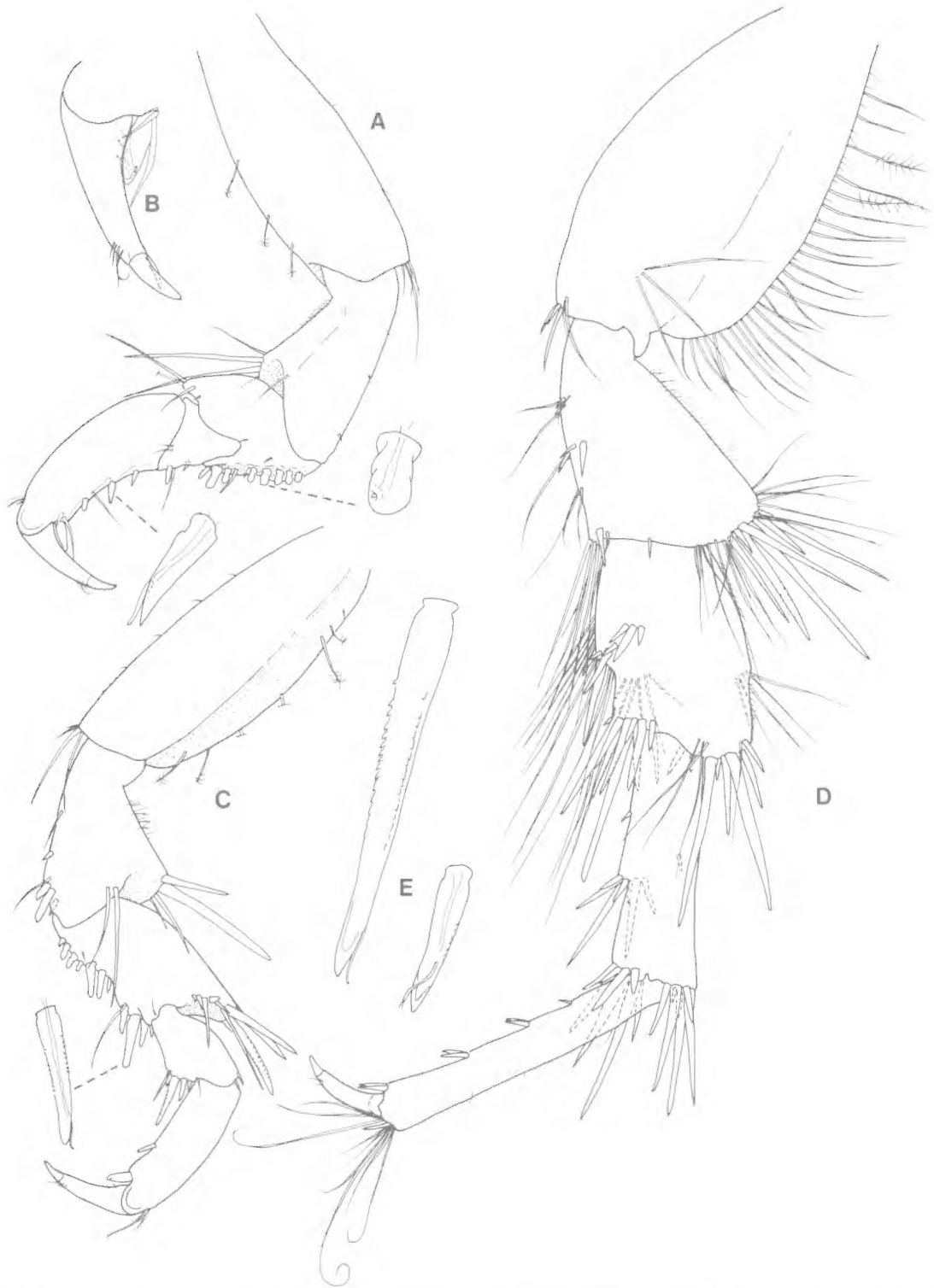


FIG. 5. *Plakolana accola* sp. nov. All figs of ♂ paratype 9.3mm. A, pereopod 1; B, dactylus, pereopod 1; C, pereopod 2; D, pereopod 7; E, spines from posterodistal angle of merus.

Pleopods as for genus. Appendix masculina with apex bent medially. Uropod exopod distinctly shorter than endopod, apex sub-bifid, lateral process prominent; lateral margin with 8-10 spines, medial with 5 spines set amongst PMS. Endopod lateral margin straight, with 5 spines, PMS for about 0.75 distal margin; medial margin with 5 spines set amongst PMS; apex sub-bifid, small spine set medially to apex.

Female. Similar to male but for: maxilliped with lamina vibrans (3 plates); pleopod endopod lobes slightly larger. Oostegites on coxae 1-5, largely overlapping; embryos retained with single large cavity formed by indentation of ventral body surface in body. Female of 29mm contained 28 ova, measuring 2.5-2.8mm in diameter.

Colour. Pale tan with abundant small reddish brown chromatophores giving a rusted appearance in life; eyes black.

Size. Males 19-32mm, non-ovigerous females 21-31mm, ovigerous females (4 specimens measured) 29-32mm. Two manca, with pereopod 7 not present, measured 7.0 and 7.7mm.

Variation. Males, females and manca present uniform appearance, but many specimens had malformed uropods and pleotelson. The spine counts presented here are based on 20 specimens, but damaged specimens have been omitted. Telson ($n=17$) with 6+6 spines (41.2%), 6+7 spines (29.4%) or 7+7 (29.4%). Exopod ($n=38$) lateral margin with 9 (47.4%), 8 (21.1%) or 10 (15.8%) spines; medial with 5 (94.7%) spines. Endopod ($n=36$) lateral margin with 5 (44.4%), 6 (41.7%) or 7 (5.6%) spines; medial margin with 5 (11.0%), 6 (63.9%) or 7 (27.8%) spines.

REMARKS

This species is readily identified and distinguished from *A. schioedtei* by the pleotelson spines being restricted to the posterior third of the pleotelson, uropod lateral margins being straight not sinuate, posterior margin of pleonite 4 being rounded not acute and in lacking an entire dorsal interocular furrow. *Aatolana rapax* never has the dorsal surface of the pleotelson setose, which occurs in large males of *A. schioedtei*.

Plakolana gen. nov.

Body smooth, unornamented. Cephalon anterior margin medially indented, without rostral point. Pereonite 1 about twice as long as 2; pleonite 1 partly or wholly concealed by pereonite 7. Pleonite 3 with epimera prominent, with postero ventral incision; longitudinal carina

with row of setae; extends posterior to pleonites 4 and 5. Telson with prominent spines and PMS.

Antennule peduncle articles 1 and 2 subequal in length, article 3 slightly longer than combined lengths of articles 1 and 2. Antenna with articles 1-3 short, 4 and 5 long, with article 5 longest. Frontal lamina slender, elongate, about 5 times longer than basal width. Mandibles with prominent spine row and molar process. Maxillule lateral lobe with stout spines on gnathal surface, medial lobe with 3 stout circumplumose spines. Maxilla with all lobes well developed. Maxilliped palp articles 2-5 with both margins setose; endite with 2 coupling hooks and prominent plumose setae.

Pereopods 1-3 with long spines at anterodistal angles of ischium and merus; pereopods 4-7 with ischium, merus and carpus, expanded, markedly flattened, abundantly provided with long spines, and long simple setae on anterior margin of basis, and posterior margins ischium and merus. All pereopods with slender secondary unguis on dactylus. Penes opening flush (or nearly so) to ventral surface of sternite 7.

Pleopod 1 peduncle quadrate, slightly longer (1.2) than wide; pleopod 2 appendix masculina attached basally. PMS present on all rami except the endopod of pleopod 5. Uropod peduncle with prominent row of simple setae along lateral margin.

Female. Maxilliped with lamina vibrans, in ovigerous specimens. Brood pouch composed of oostegites arising from coxae 1-5.

TYPE SPECIES

Plakolana accola sp. nov., here designated.

ETYMOLOGY

From the Greek *Plakos* ('anything flat and wide') combined with *-lana*. Gender is feminine.

REMARKS

The genus is characterized by having flattened and densely spined and setose posterior pereopods, slender secondary unguis on the dactylus, the unique shape of pleonite 3 (with an acute posterior point and ventrolateral incision), the elongate frontal lamina and the quadrate peduncle of pleopod 1. The flattened basis pereopods 4-7 with a row of simple setae along the anterior margin, is the only character that can be recognized as a potential unique apomorphy. Nonetheless the combination of characters delimits the genus.

Species of *Cirratulus* never have flattened posterior pereopods, nor pereopods with abundant setae or elongate spines, and the peduncle of pleopod 1 is about twice as wide as long; in



FIG. 6. *Plakolana accola* sp. nov. G, I, J, ♀ paratype 10.5mm, remainder ♂ paratype 9.3mm. A-E, pleopods 1-5 respectively; F, uropod; G, maxilliped, showing lobes; H, pleotelson apex; I, oostegite 1; J, oostegite 5.

Cirolana the cephalon has a rostral point or smoothly rounded, but never medially indented. Those species that do show some of these character (see below) are in need of redescription and their generic placement reassessed.

DISTRIBUTION

The genus is currently known from the western South Pacific.

OTHER SPECIES

Plakolana binyana (Bruce, 1991). comb.nov. Southeastern Australia.

Plakolana nagada sp.nov. Madang, Papua New Guinea.

Plakolana sp. (as *Cirolana* sp. Bruce, 1986). Eastern Australia. Known from a single immature specimen.

It is possible that *Cirolana bougartii* Kensley, 1984 belongs in *Plakolana* because the morphology of the antennule, frontal lamina, pereopods and pleopods all agree with the generic diagnosis. Characters that differ include the anterior margin of the cephalon being apparently smoothly rounded (possibly due to the perspective of the figure), pleonite 1 is largely visible, and the pleotelson and uropods are not described as having spines. This species needs further examination to assess its correct generic placement. Similarly *Cirolana stebbingi* Nierstrasz, 1931 shows a similar pleon, antennule, pereopod and pleopod morphology, and also needs to be described in detail before it can be assigned to the correct genus.

AFFINITIES

The pereopod morphology, smooth body surface, elongate pleopod 1 peduncle, and frontal lamina shape suggest that this genus is closest to *Politolana* Bruce, 1981. *Politolana* however differs in having the anterodistal margin of the ischium and merus of pereopod 1 strongly produced, in having the basis anterior margin without setae and furthermore lacks the long spines of *Plakolana*. The appendix masculina is sword shaped and sub-basally attached. In *Politolana* the antennal morphology, with peduncle articles 1 and 2 short, 3-5 long, is more similar to that of *Natatolana* than to *Plakolana* which has antennal peduncle articles 1-3 short, 4 and 5 long.

KEY TO THE SPECIES OF PLAKOLANA

- 1 Frontal lamina widest anteriorly; uropod endopod spines long (15-35% length of en-

dopod); uropod endopod distally narrowed, medial margin approximately straight 2

Frontal lamina with straight lateral margins; uropod endopod spines short (less than 12% length of endopod); uropod endopod distally wide, medial margin sinuate. 3

2. Antenna flagellum extending to pereonite 4 or 5; uropod endopod medial margin with 7 spines, distalmost spine about equal in length to adjacent spine. *P. accola*

Antenna flagellum extending to pereonite 2 or 3; uropod endopod medial margin with 5 spines, distal most of which is twice as long as adjacent spine *P. nagada*

3. Cephalon with complete dorsal interocular furrow; frontal lamina anteriorly rounded; pleotelson with 7+ spines. *Plakolana* sp.

Cephalon dorsal interocular furrow incomplete; frontal lamina distally acute; pleotelson with 4 spines *P. binyana*

**Plakolana* sp. was described from a juvenile (Bruce, 1986: 143, fig. 96). In cirolanids pleotelson spines are nearly always paired, in which case the 'normal' spination for this species would be 6 or 8.

Plakolana accola sp.nov.

(Figs 4-6)

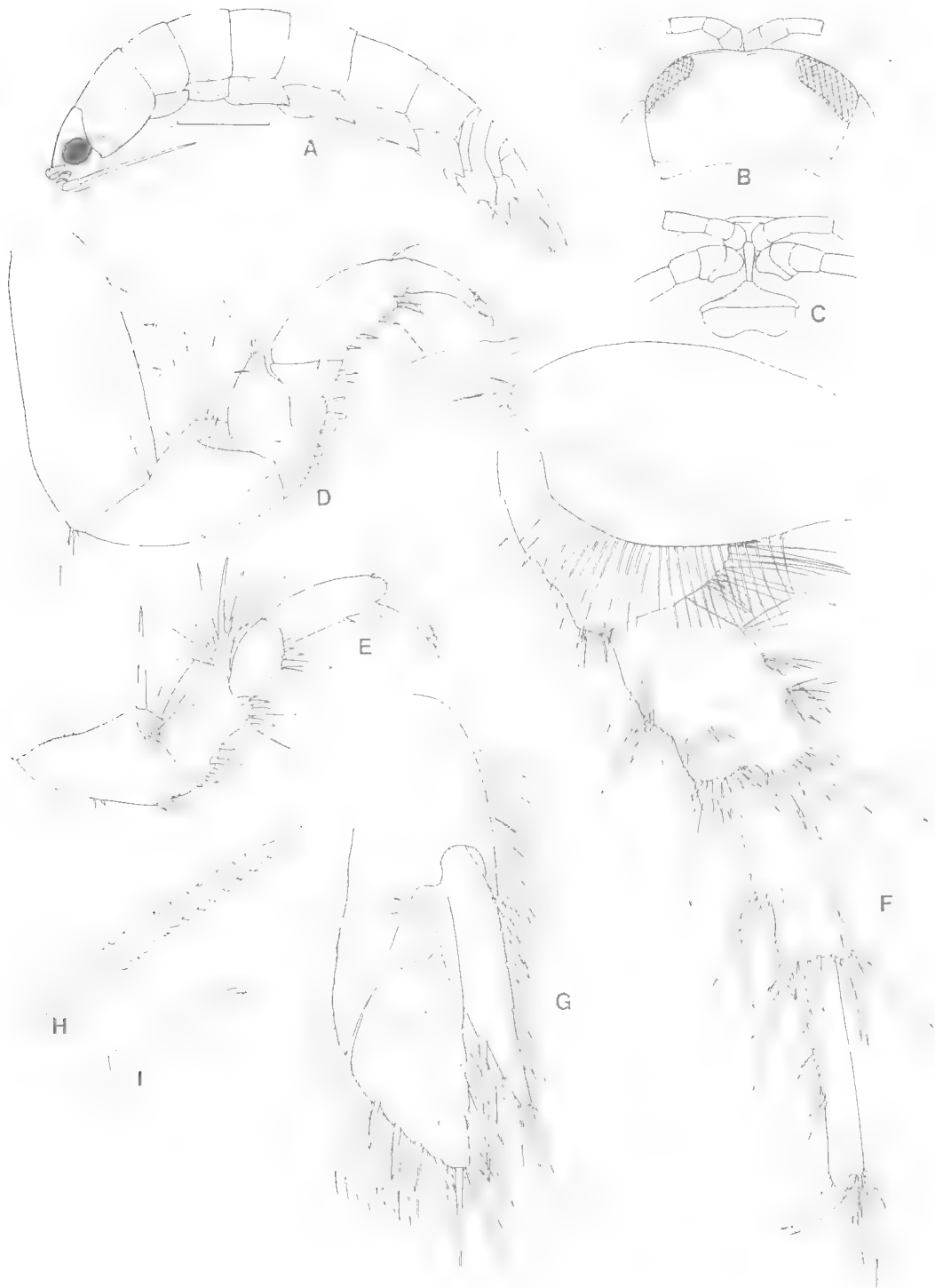
MATERIAL EXAMINED

HOLOTYPE: ♂ (9.5mm), off outer reef slope, south of Wongat Is., 5°08.4'S, 145°51.0'E, 29 Apr 1989, 300m depth, coll. N.L. Bruce & M. Jebb (QM W17993).

PARATYPES: 4♂♂ (9.3 dissected, 9.0, 7.8, 7.0mm), 9♀♀ (10.5mm ovig, 10.5, 8.0, 8.0, 7.5, 7.0, 6.5, 6.5, 6.0mm), 3 imm (5.5, 5.0, 5.0mm), same data as holotype (QM W 17994-17996). 2♂♂ (7.5, 6.8mm), ♀ (7.0 non-ovig), as for holotype but 29 Apr 1989, 450m depth (NMV J27475). 9♂♂, 5♀♀, 8 manca, off outer reef slope between Rasch Pass and Wongat Is, 5°8.7'S, 145°49.7'E, 26-27 Jan 1990; 440m depth, coll. J.K. Lowry, J. Mizeu, and J.D. Thomas (AM P40161; 1♂, 1♀ San Diego Museum).

DESCRIPTION

Body about 2.7 times as long as wide. Cephalon with anterior submarginal furrow, dorsal interocular furrow absent. Pereonite 1>2=3<4<5=6>7. Coxae of only pereonites 7 clearly visible in dorsal view. Pleon short, ca. 10% of BL, all of pleonite 1 and most of pleonite 2 concealed by pereonite 7. Pleotelson about as long as wide, lateral margin convex, converging smoothly to subacute apex; posterior margin with 6 acute spines and PMS.



Antennule peduncle article 3 longer than lengths of article 1 and 2 combined; flagellum composed of 11 articles, article 1 longest, and extending to anterior of pereonite 1. Antenna with flagellum of 32 articles, extending to anterior of pereonite 5. Frontal lamina anteriorly widest, with anterior margin rounded; about 2.5 times as long as maximum width. Mandibles with 8 (right) or 11 (left) spines on spine row; molar process with about 28 teeth; palp article 2 with about 11 simple and 4 serrate spines; article 3 with 20 spines. Maxilla with 11 spines on gnathal surface; setae on lateral and middle lobes respectively; medial lobe with 7 plumose setae (proximal) and 5 simple setae. Maxilliped with simple setae on lateral shorter, those of article 5 serrate and simple; endite with 5 long circumplumose setae.

Pereopod 1 with 4 setae at posterodistal angle of basis; 3 terminally plumose setae on anterodistal margin; ischium posterior margin with 2 small spines, anterodistal angle with 3 long setae; merus with 7 blunt tubercular spines and 2 acute spines on posterior margin, anterodistal angle with 3 setae, carpus posterior margin with 2 spines and single seta; propodus with 3 spines on palm, 4th large spine opposing base of dactylus; dactylus without distinct secondary unguis. Pereopod 2 with long spines at anterodistal angles of ischium and merus; ischium posterior margin with 2 setae and 1 acute spine, distally with 2 blunt spines; merus posterior margin with 1 long seta and 1 stout spine; carpus with 4 spines, 1 long, and 2 setae; propodus with 1 spine on palm, 1 opposing dactylus. Pereopod 7 basis with margins convex, posterior margin with about 28 feebly PMS; ischium carpus with large clusters of long spines and simple setae at distal margins; posterior margin ischium and merus with 2 and 1 cluster of spines, merus with long setae; propodus with 3 groups of paired spines and a single spine proximally; anterodistal angle with long setae.

Pleopod 3-5 exopods with partial suture only. Uropod peduncle with prominent row of setae on lateral margin; with single lateral spine and 2 spines at distoventral angle; exopod lateral margin with 5 prominent and 1 small subapical spine, medial margin with 4 spines, distal spine not much larger than adjacent spine; endopod lateral margin weakly sinuate, with 3 prominent spines, longest 18% length of lateral margin, and 1 small subapical spine, medial margin with 7 spines, distal spine not much larger than adjacent spine.

All margins with PMS, except proximal half (0.45) of endopod lateral margin without setae.

Female: Similar to male; oostegites on coxae 1-5; maxilliped with lamina vibrans (3 plates). Females with embryos not observed.

Colour: White to translucent in life and alcohol; chromatophores absent. Eyes pale, reddish brown to yellow.

Size. Males 7.0-9.5 (mean = 8.1, $n=7$), females 6.0-10.5 (mean = 7.8, $n=10$), manca up to 5.5mm.

Variation. Pleotelson and uropod spine counts were near constant. Exopod ($n=23$) lateral margin with 5 prominent spines (95.6%), medial margin with 4 spines (64.7%) or 5 (29.4%). Endopod ($n=23$) lateral margin with 3 prominent spines (100%), medial margin with 6 (8.7%), 7 (86.9%) or 8 (4.3%).

REMARKS

Plakolana accola can be distinguished from others of the genus by the short pleon which has segment 1 and most of 2 concealed by pereonite 7. *P. binyana* from southern Australia has the frontal lamina with a narrow anterior margin and broader uropods which have far shorter spines. *P. nagada*, which occurs in shallow water within the barrier reef system at Madang, is readily distinguished by a longer pleon, longer spines on the uropods, and by having the distalmost spine on the medial margin of each uropod ramus far longer than the adjacent spine.

DISTRIBUTION

Outer reef slope at Madang, between 300 and 450m depth.

ETYMOLOGY

Accola is a Latin word meaning neighbour.

Plakolana nagada sp. nov.

(Figs 7, 8)

MATERIAL EXAMINED

HOLOTYPE: ♂ (6.9mm), east of CK1 jetty, Nagada Harbour, 5°09.6'S, 145°48.7'E, 2 Feb 1990, 16m depth, soft mud bottom, coll. J.K. Lowry and J.K. Elliot (AM P41015).

PARATYPES: ♂ (7.8mm, dissected), 5 ♀♀ (8.0 dissected, 7.5, 7.3, 7.2, 7.2mm), imm (4.9mm), same data as holotype (AM P40172). ♀ (7.1mm, ovig), south of

FIG. 7. *Plakolana nagada* sp. nov. A-C, holotype, remainder ♂ paratype 7.8mm. A, lateral view; B, cephalon; C, frons; D, pereopod 1; E, pereopod 2; F, pereopod 7; G, uropod; H, spine, distal margin of merus; I, short spine, anterodistal angle of carpus. Scale represents = 1.0mm.

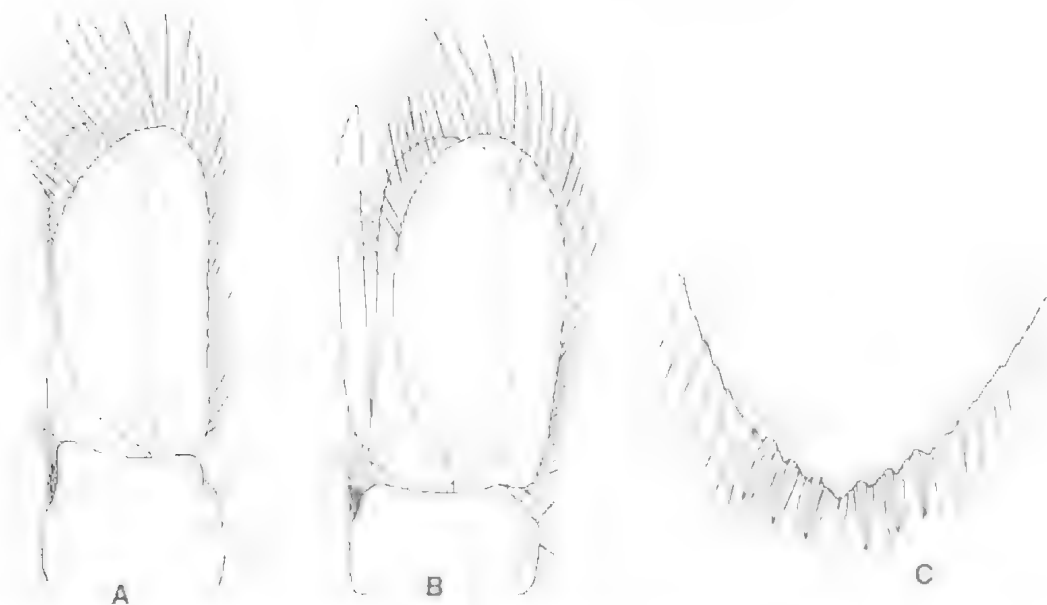


FIG. 8. *Plakolana nagada* sp. nov. All figs of ♂ paratype 7.8mm. A, pleopod 1; B, pleopod 2; C, pleotelson apex.

Tripod Reef, 5°09.7'S, 145°51.3'E, 30 Apr 1989, 22m depth, on sand, coll. N.L. Bruce (QM W18001).

DESCRIPTION

Pleon about 12.5% BL, pleonite 2 largely visible. Pleotelson with 6 spines.

Antenna flagellum extending to posterior of pereonite 3.

Pereopod 1 merus posterior margin with 6 blunt spines and 2 short acute spines. Pereopod 2 merus posterior margin with 1 long seta and 8 stout spines. Pereopod 7 merus with 3 clusters of setae on anterior margin; posterior margin with 2 ranks of simple setae.

Uropod exopod lateral margin with 5 prominent and 1 small subapical spine; medial margin with 4 spines, proximal two longest, distal spine distinctly longer than adjacent spine. Endopod lateral margin with 3 prominent and 1 small subapical spine; 2 longest spines are 32 and 35% length of lateral margin; medial margin with 5 spines, distalmost spine about twice as long as adjacent spine.

Colour. Pale brown in alcohol; eyes pale brown.

Size. Adults 6.9 - 8.0mm.

Variation. Pleotelson and uropod spine counts are near constant. Exopod lateral margin with 5 large and 1 small (100%); medial margin with 4 spines, 3 once. Endopod lateral margin 3 large

spines and 1 small (86.6%) or with 2 large spines (13%); lateral margin with 5 (54.5%) or 6 (45.5%) spines (n=15 for all percentages). Pleotelson posterior margin with 6 (62.5%) or 5 (37.5%) spines (n=8).

REMARKS

Plakolana nagada is very similar to *P. accola*, but differs both in habitat (inshore, shallow sedimentary bottom compared to deeper reef slope) and numerous morphological features.

P. nagada in the first instance has much longer pereopod and uropod spines, and also has more of the pleon visible. Specifically the two species can be separated by *P. nagada* having most of pleonite 2 visible, 5 spines on endopod medial margin (vs 7), the terminal spines on the endopod and exopod medial margins being far longer than the adjacent spine, and the spines on the lateral margin of the endopod being much longer (32-35% ramus length vs 18% in *P. accola*).

DISTRIBUTION

Shallow muddy and sand bottoms within the barrier reef at Madang; recorded depths 16 and 22m.

ETYMOLOGY

The epithet is taken from the type locality, and treated as a noun in apposition.

ACKNOWLEDGEMENTS

This contribution was made possible by a Christensen Research Institute Fellowship, for which I thank the Christensen Fund. I also thank Dr Matthew Jebb for his considerable field assistance.

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FIRST RECORD OF CTENOPHORE COELOPLANA (BENTHOPLANA) METEORIS (THIEL, 1968) FROM AUSTRALIA. *Memoirs of the Queensland Museum* 33(1). 16. 1993:— There are only two records of benthic ctenophores (Ctenophora: Platyctenida) from Australian waters: *Coeloplana* sp. and *C. cf. willeyi* Abbott, 1907 (Stephenson et al., 1931; Smith & Plant, 1976). I record here a third species, *Coeloplana (Benthoplana) meteoris* (Thiel, 1968), previously known from Somalia, east Africa (08°26.2'N, 50°20.2'E) (Thiel, 1968) and NW Madagascar (13°24'40"-13°35'15"S, 47°48'50"-48°19'10"E) (Fricke & Plante, 1971). The specimens were collected while diving at 12-13m depth in Pioneer Bay, Orpheus Island, NEQ (18°36'S, 146°29'E). Two specimens were preserved (Queensland Museum G35888). The following description is based primarily on living animals in which taxonomic features are clearest.

The animals were living free on terrigenous muddy-sand. They had a characteristic body profile with erect tentacular horns (see Thiel, 1968, figs 1,2; Fricke & Plante, 1971, pl.1). The aboral surface was covered by a yellowish-white reticulate pattern. Fine red pigment occurred on the aboral surface above the meridional canals, around the tentacle sheaths and marginal ampoules. One live specimen, when expanded on glass, measured 36 × 31 mm. The preserved specimens measure 8 × 10 and 10 × 16 mm.

The apical organ had four polar fields, which were multiply branched (see Fricke & Plante, 1971, fig. 3). The fields did not contract, however, as observed by those authors.

Tentacles were typical with a primary axis and tentilla. They extended from beneath the tip of the tentacular horn, i.e., the opening of the tentacle sheath was oral.

The preserved specimens are folded along the tentacular axis; a faint crease runs along the oral surface from the mouth to the base of the tentacular horns, but no oral groove or oral lappets were seen.

The following description of the gastrovascular system uses the terms of Thiel (1968). Radial canals gave rise on either side to 2 pairs of adradial canals that led directly to the meridional canals. There were 3-4 digitate to trifid aboral papillae over each of the meridional canals. A pair of subparallel tentacular canals ran on either side of the tentacle sheath, arising beyond the distal adradial canals. The peripheral gastrovascular system branched dichotomously to form a complex network, best developed on the oral surface.

Cydidippid larvae were found next to the meridional canals (the specimens were collected in January). Peripheral sacs were each connected by a transparent tube to a marginal pore. These seem to be testicular ampoules (see Fricke & Plante, 1971).

Body profile, marginal position of tentacle sheath openings and variable aboral papillae are consistent with *Vallidula* Rankin, 1956 and some species of *Coeloplana* Kowalevsky, 1880 as defined by Fricke (1970), Harbison & Madin (1982) and Rankin (1956). However, I did not see the oral lappets, oral groove, spherical vesicle of the gastrovascular system or additional cross-piece of the tentacular sheath that characterize *Vallidula*.

Of the 21 nominal species of *Coeloplana* (Fricke, 1970), three have a gastrovascular system similar to that in my specimens: *C. perrieri* Dawydoff, 1938, *C. mesnili* Dawydoff, 1938 and *C. meteoris* Thiel, 1968 (Thiel, 1968; Fricke & Plante, 1971). All were reported as free living (*C. mesnili* in

the plankton, *C. perrieri* on rocks and seagrass, *C. meteoris* on soft-sediment). The present specimens differ from *C. mesnili* and *C. perrieri* (Dawydoff, 1938a,b) in body profile, position of openings of the tentacle sheath and testes, colour pattern, structure of the apical organ and aboral papillae. They conform well with *C. meteoris* in (1) the free-living habit on soft-sediment, (2) high body profile with tentacular horns, (3) oral openings of the tentacle sheath, (4) distinctive apical organ with four polar fields, (5) tentacular canals bifurcating beyond the distal adradial canals, (6) colour pattern, (7) complex aboral papillae, and (8) marginal position of ampoules (otherwise known only from *Ctenoplana (Diploctena) neritica* Fricke & Plante, 1971). This combination of features was so distinctive that Fricke & Plante (1971) created a new subgenus, *Benthoplana*, for *C. meteoris*.

This record considerably extends the range of *C. meteoris*. Fricke & Plante (1971) showed it can be abundant (up to 64/m²). The paucity of published records probably reflects the lack of direct observations in soft-sediment habitat.

Specimens were collected during a study on soft-sediment epibenthos with Dr R.A. Birtles (James Cook University), funded by an Australian Marine Sciences and Technology grant. I thank Drs A. Birtles and C. Wallace for their comments.

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Peter Arnold, Museum of Tropical Queensland, 70/84 Flinders St, Townsville, Queensland 4810, Australia; 15 October, 1992

NEW TEMNOCEPHALANS (PLATYHELMINTHES): ECTOSYMBIONTS OF FRESHWATER CRABS AND SHRIMPS

L.R.G. CANNON

Cannon, L.R.G. 1993 06 30: New temnocephalans (Platyhelminthes): ectosymbionts of freshwater crabs and shrimps. *Memoirs of the Queensland Museum* 33(1): 17-40. Brisbane. ISSN 0079-8835.

Six new species of *Temnocephala* are described from freshwater crabs and shrimps from Queensland, *Temnohaswellia* Pereira & Cuocolo, 1941 is re-erected for two new species with 6 tentacles and *Achenella* n. gen. is proposed for two new species of worms with only one pair of testes. This is the first time temnocephalans have been reported from crabs and shrimps in Australia. □ *Temnocephala*, *Temnohaswellia*, *Achenella*, *ectosymbiont*, *crab*, *shrimp*.

Lester R.G. Cannon, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 2 November, 1992.

Temnocephalans are small ectosymbiotic flatworms which are known from a variety of freshwater invertebrates from mainly South America and Australia. Their taxonomic status has shown some variation (Williams, 1981), but they are generally considered to be close to the dalyellioid turbellarians. The Australasian region seems the centre of diversity (Cannon, 1991), but here the diversity of hosts recognised has been low, i.e., they have been reported almost exclusively from crayfish of the family Parastacidae. Crabs and shrimps have been reported as hosts in southern Asia and South America; however, this is the first such report from Australia.

Crabs and shrimps were trapped or collected in dip nets from streams and ponds throughout eastern Australia. Hosts were retained for short periods until the hosts could be examined in the field or laboratory with a dissecting microscope and the worms removed into clean water. Worms were fixed when possible in 10% cold buffered formalin, AFA (alcohol, formalin and acetic acid), SUSA or Bouin's fluid; some were obtained from hosts fixed in 70% alcohol or from hosts killed by near boiling water. Whole mounts were stained with Mayer's haemalum or Harris' haematoxylin and mounted in Canada balsam. Serial sections were obtained from worms embedded in 56°C Paraplast and cut at 5-7µm and stained with Mayer's haematoxylin and eosin, though occasionally Mallory's trichrome was used.

Descriptions were prepared with the aid of DELTA (Dallwitz & Paine, 1986). Over 130 characters were designated, though not all were applicable to all descriptions, e.g. egg capsule characters were not included if egg capsules were

not found. With limited material of some species and variation in the quality of fixation dependent upon the immediacy of treatment some characters are included as 'inconspicuous', '(absent?)' or simply qualified with '(?)'. All measurements were obtained with the aid of a camera lucida. Material is deposited in the collections of the Queensland Museum (QM) and wholemounts are designated (W) and serial sections (LS, TS or FS -longitudinal, transverse or facial sections: the number of slides in the series given in []).

Abbreviations used in figures: c cirrus, dg disc glands, e eye, es ejaculatory sac, ex excretory ampulla, g gut, ga genital atrium, gc genital capsule, gp gonopore, Hc Haswell's cells, og ootype gland, ov ovary, ph pharynx, plg postero-lateral glands, pr prostate, rg rhabdite glands, ro rosette organ, sg shell glands, sr seminal receptacle, sv seminal vesicle, t testis, v vagina, vit vitellaria, vitd vitelline duct, vr vesicula resorbens.

TERMINOLOGY

Hickman (1967) drew attention to the variety of names used for various parts of the reproductive organs of temnocephalans. I happily accept the term vesicula resorbens (not resorbens) for this structure described in detail by Haswell (1924). Earlier I have tried to provide a consensus regarding the terminology relating to all turbellarians (Cannon, 1986). Within the male temnocephalan I agree with Haswell (1893) and Baer (1953) that the swollen part of the system storing sperm prior to release is appropriately called the seminal vesicle. The ejaculatory duct leaves the seminal vesicle distally and enters the (usually muscular) base of the intromittent organ. Haswell

(1893) called this muscular base the cirrus bulb, but since this is where the prostate glands join the ejaculatory duct and surround it 'prostate bulb' (or simply 'prostate') is the most appropriate functional term. The prostate is sometimes no wider than the sclerotic base of the male organ, but may be a much enlarged bulb.

As Baer (1953) pointed out, Australian species of temnocephalans also have an additional sac, evidently absent from South American species. This is variably developed: in some it is a discrete sac or vesicle opening, via a narrow duct, into the prostate adjacent to the ejaculatory duct; in others it is merely a proximal extension from the prostate beyond the ejaculatory duct entrance. Haswell (1893) called this the ejaculatory sac, a term I accept. Hickman (1967) called it a prostate vesicle mistakenly attributing this term to Baer (1953) who called such a structure in *Diceratocephala boschmai* a prostate, but said 'elle est sans doute homologue de la vesicle ejaculatrice des autres Temnocephales'. This sac is frequently empty or contains only a few sperm; it does not contain prostatic secretion.

The male intromittent organ in most temnocephalans consists of a hard sclerotic tube the terminal part of which has spines or more often rows of spinelets which are eversible. The terminal part may or may not be enlarged. Haswell (1893) called the organ a cirrus and the terminal part the introvert. Cirrus is the appropriate term for a spiny eversible male organ. The basal rigid section could be considered a stylet, but is here called the shaft, and the term 'cirrus' of Haswell is accepted here, not 'penis' as used by Hickman (1967).

Finally, in many temnocephalans there are distinctly staining cells anterior to or adjacent to the brain. Haswell (1893) first referred to them as 'problematic cells'. They have also been called 'schokoladenbraune Drüsen' (see Cannon, 1991). Hickman (1967) figures and describes these cells which he says may be paranephrocytes, though cautiously, as these latter are wandering cells: the cells in question are constant in position. There are often two pairs and their position near the brain suggests they may be neurosecretory. Until a function can be ascribed I propose to call them Haswell's cells.

Family TEMNOCEPHALIDAE Monticelli,
1899

Temnocephala Blanchard, 1849

Generic diagnosis. Temnocephalidae with five

anterior tentacles, a posterior adhesive disc and paired lateral testes.

Temnocephala athertonensis n.sp.
(Figs 1.1 (a-c))

MATERIAL EXAMINED

HOLOTYPE: exocarpace of *Holthuisana agassizi* (Sundathelphusidae), Rocky Ck, nr Carbeen (17.11.2°S, 145.26.8°E), 26 Sep. 1990, L. Cannon & K. Sewell. Hot water/AFA/Hx GL14562 (W).

PARATYPES: same data as holotype, AFA/Hx GL14563-7 (W); Hot water/Bouin's/H&E GL14569 (LS[2]); Hot water/AFA/H&E GL14570 (LS[2]); Hot water/Bouin's/Mallory's GL14571 (LS[1]).

OTHER MATERIAL: same data as holotype, AFA/Hx GL14568 (W); Hot water/Bouin's/Mallory's GL14572 (LS[1]); Bouin's/H&E GL14573 (LS[2]); Hot water/AFA/H&E GL14574 (LS[2]); Bouin's/Mallory's GL14575 (LS[1]).

DESCRIPTION

External characteristics. Body about 1.2-2mm (mean=1.7mm) long, and about 0.5-0.9mm (mean=0.7mm) wide; oval or elliptical, dorso-ventrally compressed, but without flanges, or not dorso-ventrally compressed. Pigment creates impression of grey, actually a well defined pattern: dorsally a tracery extends from the base of the tentacles posteriorly and laterally to near the body margins, but becomes less dense towards the posterior. The pigment extends through the body outlining nerve tracts and major structures, and some is seen ventrally especially anterior to the mouth. Posterior adhesive disc pedunculate: disc diameter 280µm at rim, disc peduncle about 145µm in diameter. Epidermis syncytial with scattered nuclei, about 5-6µm high dorsally and ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ventrally, as wide as long, about 180µm in diameter; strong, divided into anterior and posterior sphincter blocks by a region containing nucleated cells but few muscle fibres; lacking a non-cellular lip, with a conspicuous non-cellular lining (extending to buccal region), muscles not forming an obvious crenulate buccal rim. Pharynx sphincters slightly stronger posteriorly. Oesophagus inconspicuous. Gut darkly coloured, longer than wide to as wide as long; with ill-defined septa. Gastrodermis about 90µm high. Gut with diatoms.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick

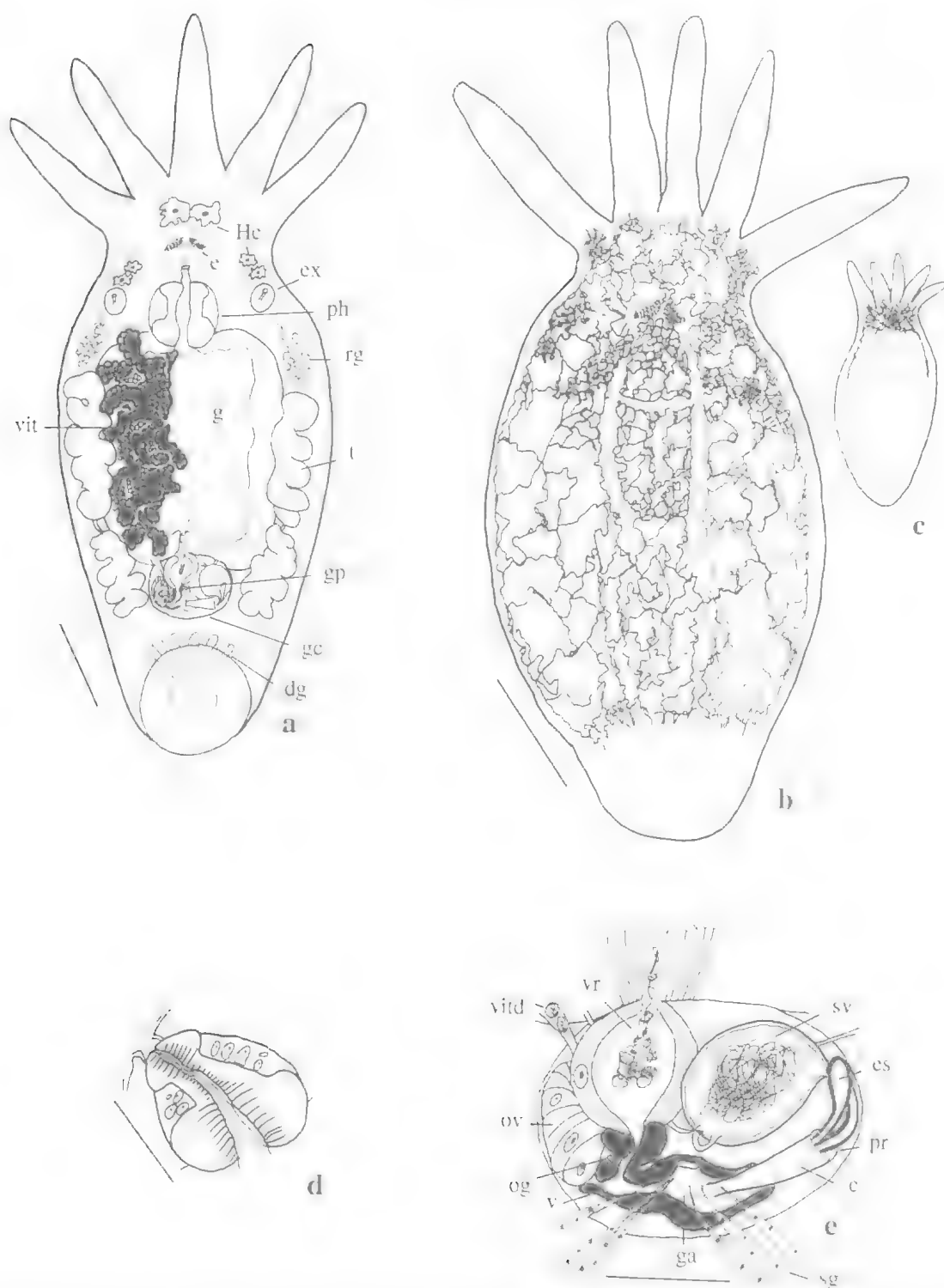


FIG. 1. *Temnocephala athertonensis* n.sp. a, internal anatomy of whole animal; b, dorsal pigment pattern; c, ventral pigment pattern; d, pharynx; e, detail of genital capsule. Scales: a,b, 250 μ m; c, not to scale; d,e, 100 μ m.

walled, about 75µm in diameter. Major excretory ducts conspicuous posterior to ampullae.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks conspicuous in sections although pigment pattern outlines some. Eyes present, adjacent, with pigment mesh forming a single dark region, each about 40×25µm. Eye pigment granules irregular, mostly small (extremely fine), red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes, numerous, 10 or more each side; each about 30µm across, with inconspicuous rhabdite tracts. Rhabdites only accumulate on tentacles. Haswell's cells conspicuous, six, a pair before brain, beside brain and before excretory pores (but median and lateral glands close together), each of the larger anterior pair irregular and about 50µm across, median pairs, smaller, about 30-40µm across. Oesophageal glands inconspicuous (absent?). Ootype glands present (restricted to a small field). Shell glands present (a small group of eosinophilic glands posterior to gonopore). Postero-lateral glands present, but difficult to see in whole mounts. Disc glands prominent, a discrete cluster.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles weak. Attachment muscles of pharynx weak. Attachment muscles of adhesive disc moderately strong. Muscles controlling male organ strong immediately about the cirrus.

Reproductive system ♀. Gonopore mid-ventral, in posterior quarter of body. Genital atrium commodious. Genital complex contained in a connective tissue capsule. Ovary about 70µm in diameter. Vesicula resorbens present, about 80-100µm across, 15µm thick wall, with strong muscular duct or sphincter joining it to vagina, lying free of gut wall (in capsule), can open to gut. Seminal receptacles not present. Vagina strongly muscular, becoming less so proximally. Vitellaria dendritic, dorsal to ventral.

Reproductive system ♂. Testes elliptical; anterior about 170×230µm, lobulate, lateral to gut, posterior about 140×210µm, lobulate, lateral or posterior to gut. Vasa deferentia narrow, entering seminal vesicle separately. Seminal vesicle about 100µm in diameter. Ejaculatory sac present, with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft gently curved. Cirrus hardly tapering, 80µm long, 35µm wide at base. Cirrus introvert not swollen, about

15µm or 1/6 length, only a weak collar of spinelets. Cirrus spinelets minute, few rows, i.e. <20.

ETYMOLOGY

The specific name pertains to the locality.

REMARKS

These worms from small freshwater crabs resemble most closely *T. minor* Haswell, 1888, the only species described with a grey tracery of pigment. The present species is only half the size of *T. minor* and the cirrus completely lacks the swollen introvert of that species. Furthermore, Haswell (1893) makes no mention of a capsule surrounding the genital organs, a characteristic of the present species. The pharynx of the present species is also distinctive. Postero-lateral glands are present, but barely discernible. The only species described with such glands is *T. chaeropsis* Hett, 1925 from the crayfish '*Chaerops preissi*' (an old name: several species are now recognised from WA) from the region of Mammoth Cave, WA. In that species, however, the glands are conspicuous, adjacent and, furthermore, the worms lack conspicuous pigment except for the eyes (Hett, 1925).

Temnocephala butlerae n.sp. (Figs 2, 11d)

MATERIAL EXAMINED

HOLOTYPE: ex carapace *Holthuisiana transversa* (Sundathelphusidae), Bore drain, Augathella (25°48'S, 146°35'E), 20 Apr. 1987, S. Butler, AFA/Haemalum GL14558 (W).

PARATYPES: same data as holotype, AFA/Hx GL14559 (W); Bouin's/H&E GL14560 (LS[3]).

OTHER MATERIAL: same data as holotype, AFA/H&E GL14561 (LS[1]).

DESCRIPTION

External characteristics. Body about 1.5mm long, and about 0.66mm wide; oval or elliptical, dorso-ventrally compressed, but without flanges. Pigment a light tracery over most of dorsal surface, extends to ventral surface (below eyes anterior to mouth). Posterior adhesive disc pedunculate: disc diameter 300µm at rim, disc peduncle 150µm in diameter. Epidermis syncytial, about 4µm high dorsally and ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous. Pharynx directed antero-ventrally, as wide as long, and about 160µm in diameter;

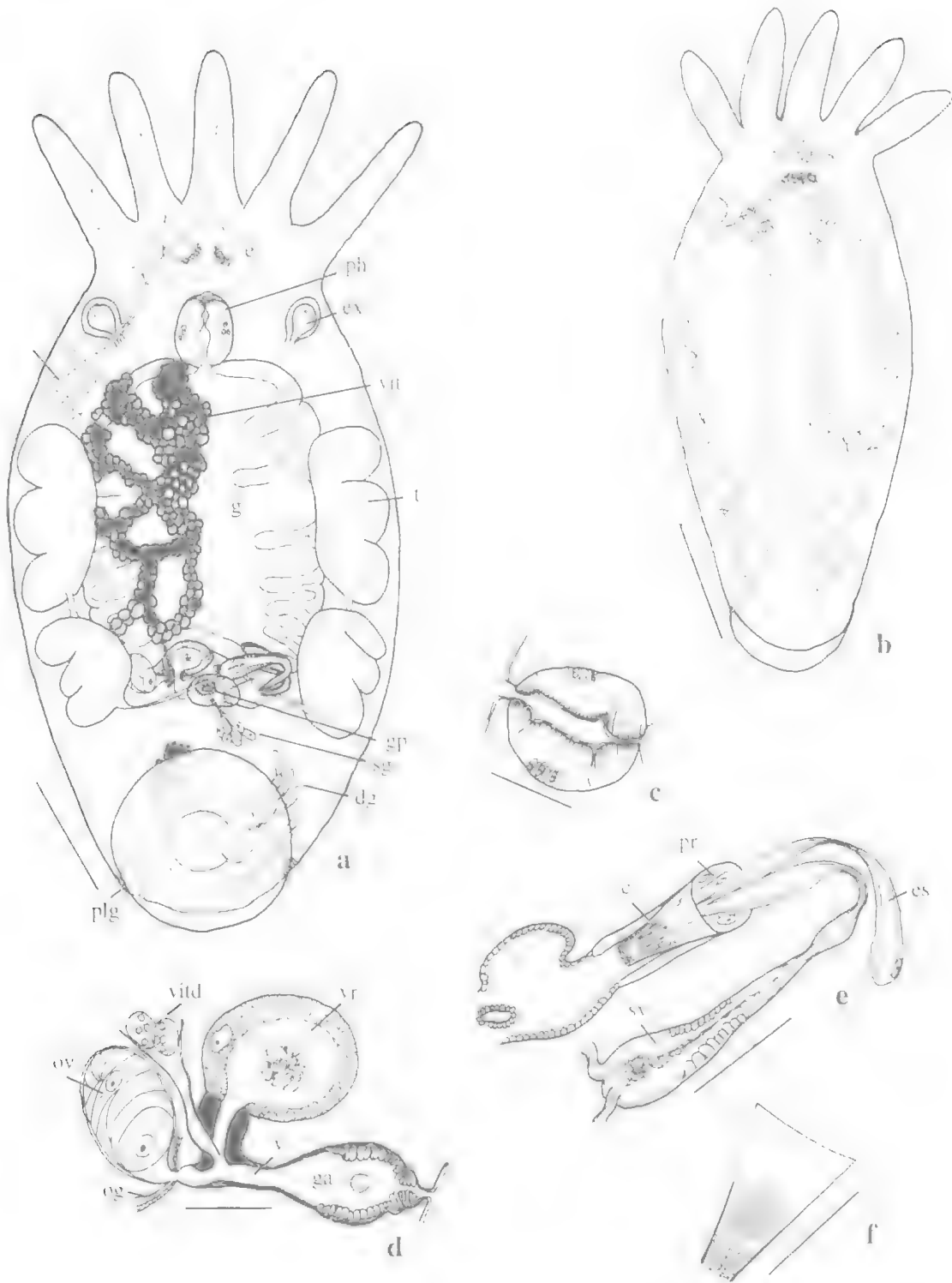


FIG. 2. *Temnocephala butlerae* n.sp. a, internal anatomy of whole animal; b, dorsal pigment pattern; c, pharynx; d, detail female reproductive system; e, detail male reproductive system; f, cirrus. Scales: a,b, 250 μm; c-e, 100 μm; f, 50 μm.

strong, divided into anterior and posterior parts, containing nucleated cells within muscle blocks (concentrated between first and second blocks); lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles forming a crenulate buccal rim. Pharynx sphincters stronger posteriorly. Oesophagus inconspicuous. Gut darkly coloured, longer than wide, weakly septate. Gastrodermis about 20-40 μm high (numerous large cells filled with eosinophilic granules lie in gastrodermis).

Excretory system. Excretory pores posterior to mouth. Excretory ampulla a simple vacuole, thick walled (9-10 μm), about 90 μm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band (20 μm wide). Major nerve trunks inconspicuous. Eyes present, adjacent, with pigment mesh forming a single dark region, each about 35 \times 25 μm . Eye pigment granules irregular, mostly small, red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes (well formed, resembling a bunch of grapes), numerous, 10 or more each side; each about 30 μm in diameter, with prominent rhabdite tracts to tentacles. Rhabdites evident in ventral epidermis (anteriorly, as well as on tentacles). Two Haswell's cells outlined by pigment. Oesophageal glands prominent. Ootype glands present (not well developed). Shell glands present (eosinophilic, lying posterior to gonopore). Postero-lateral glands present (well developed, but hard to see as they are refractory to haematoxylin and eosin stains). Disc glands present (long tracks spread from peduncle/posterior body to discharge over the disc surface).

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles, attachment muscles of pharynx, of adhesive disc and those controlling male organ all weak.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium commodious (sphincter present and muscular festoons about the walls). Genital complex scattered. Ovary about 80 \times 50 μm . Vesicula resorbens present, about 100 \times 60 μm , with 15 μm thick wall, strong muscular duct or sphincter joining it to vagina; lying free of gut wall, not open to gut. Seminal receptacles not present. Vagina short, inner region weakly muscular, opening directly to atrium. Vitellaria dendritic, dorsal to ventral.

Reproductive system ♂. Testes elliptical; ante-

rior about 270 \times 200 μm , lobulate, lateral to gut; posterior) about 230 \times 210 μm , lobulate, posterior or postero-lateral to gut. Vasa deferentia swollen, entering seminal vesicle separately. Seminal vesicle 95 \times 55 μm , with long reflexed ejaculatory duct from it to base of cirrus. Ejaculatory sac present (long), with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft straight. Cirrus strongly tapering, about 70 μm long, about 54 μm wide at base. Cirrus introvert not swollen, weakly sclerotic, inner surface thrown in to fine ridges becoming a few rows of spinelets.

ETYMOLOGY

The specific name refers to the collector, Dr Shirley Butler.

REMARKS

As with *T. athertonensis* there is a tracery of pigment over the dorsal surface which resembles only one previously described species, *T. minor* Haswell, 1888. The nature of the cirrus and the presence of the postero-lateral glands separates it clearly from *T. minor*. It is close to *T. athertonensis*, but differs in having much finer pigment, a pharynx with a stronger central muscle region, a less muscular vagina, a small, broad cirrus, and most obviously in lacking the conspicuous capsule about the genital organs.

Temnocephala improcera n.sp. (Figs 3, 11c)

MATERIAL EXAMINED

HOLOTYPE: ex *Caridina indistincta* (Atyidae), Murray R., nr Kiriama (18.01°S, 145.53°E), 26 Jul. 1984, L. Winsor, Form./H&E GL14576 (LSJ2).

PARATYPES: same data as holotype, Form./Mallory's GL14577 (LSJ1).

OTHER MATERIAL: same data as holotype, Form./Hx GL14578 (damaged W).

DESCRIPTION

External characteristics. Body about 700 μm long, and 350 μm wide; oval or elliptical, not dorso-ventrally compressed. Pigment extends through body, prominent on dorsal and ventral surfaces. Posterior adhesive disc pedunculate; disc diameter 230 μm at rim, disc peduncle about 100 μm across. Epidermis syncytial, 3.5 μm high dorsally, 5.5 μm high ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx

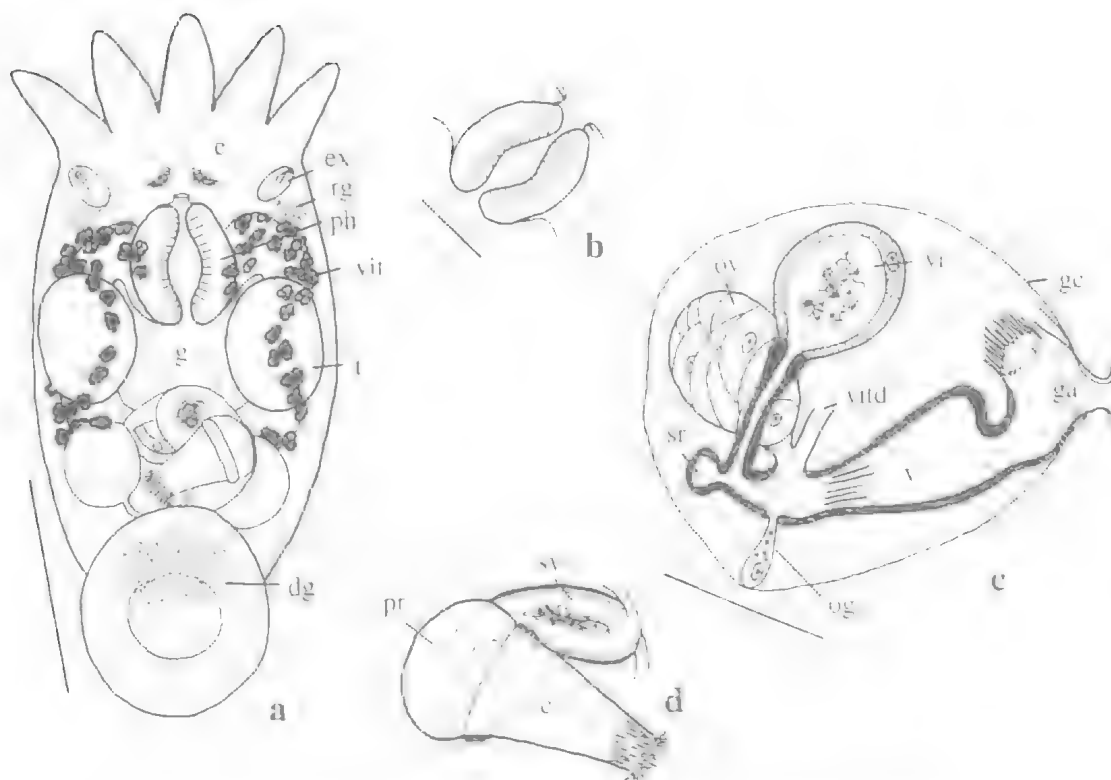


FIG. 3. *Temnocephala improcera* n.sp. a, internal anatomy of whole animal; b, pharynx; c, detail of female reproductive system; d, detail of male reproductive system. Scales: a, 250 μ m; b, c-d, 100 μ m

inconspicuous. Pharynx directed antero-ventrally, as wide as long, about $145 \times 130 \mu$ m; strong, undivided, with a few tiny eosinophilic glands in the muscle block; lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles not forming an obvious crenulate buccal rim. Pharynx sphincters equal. Oesophagus inconspicuous. Gut darkly coloured (filled with brown globular (about $5\text{--}10 \mu$ m) inclusions), longer than wide; with septa. Gastrodermis 60μ m high.

Excretory system. Excretory pores anterior to mouth. Excretory ampulla a simple vacuole (but elongate), thick walled ($12\text{--}14 \mu$ m), about $70 \times 30 \mu$ m.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, discrete, well separated, about $20 \times 30 \mu$ m. Eye pigment granules irregular, mostly small, black-brown.

Glands. Rhabdite glands in lateral fields anterior to anterior testes. Rhabdites only accumulate on tentacles (?). Haswell's cells and oesophageal glands inconspicuous (absent?). Ootype glands

present. Shell glands and postero-lateral glands absent. Disc glands conspicuous, filling the posterior body.

Muscles. Longitudinal muscles of body wall stronger ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles weak. Attachment muscles of pharynx weak. Attachment muscles of adhesive disc strong. Muscles controlling male organ weak.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium small. Genital complex contained in a connective tissue capsule. Ovary about $120 \times 60 \mu$ m. Vesicula resorbens present, about $70 \times 35 \mu$ m, 7μ m thick wall; lying free of gut wall, not open to gut. Seminal receptacle single. Vaginal teeth absent. Vagina long, compartmentalised. Vitellaria scattered laterally, dorsal to ventral.

Reproductive system ♂. Testes rounded: anterior about 150μ m in diameter, smooth, lateral to gut, posterior about 100μ m in diameter, smooth, lateral or postero-lateral to gut. Vasa deferentia narrow, entering seminal vesicle separately. Seminal vesicle about $35 \times 100 \mu$ m. Ejaculatory

sac absent (?). Prostate bulb separate, i.e. wider than cirrus base. Cirrus shaft straight. Cirrus hardly tapering, 100 μ m long, 70 μ m wide at base, with basal collar. Cirrus introvert not swollen, about 25 μ m or 1/4 of the cirrus length. Cirrus spinelets moderately sized, filling inside, few rows, i.e. <20.

ETYMOLOGY

From *improcerus* L. = short, referring to the cirrus.

REMARKS

The combination of a pigmented body and the presence of a genital capsule means this species resembles most closely *T. athertonensis* (see above). However, it is much smaller, lacks the postero-lateral glands (though these are poorly

developed in *T. athertonensis*), has smooth not lobulate testes, possesses a single seminal receptacle and has a short broad cirrus with a distinctive basal collar: none of these characters are shared with *T. athertonensis*.

Temnocephala minuta n.sp. (Fig. 4)

MATERIAL EXAMINED

HOLOTYPE: ex *Paratya australiensis* (Athyidae), Sandy Ck tributary of Dawson R. nr Taroom (25.39°S, 149.48°E), 3 Dec. 1986, L. Cannon & J. Jennings, AFA/Haemalum., GL14555 (W).

PARATYPE: same data as holotype, AFA/H&E GL14556 (LS[2]).

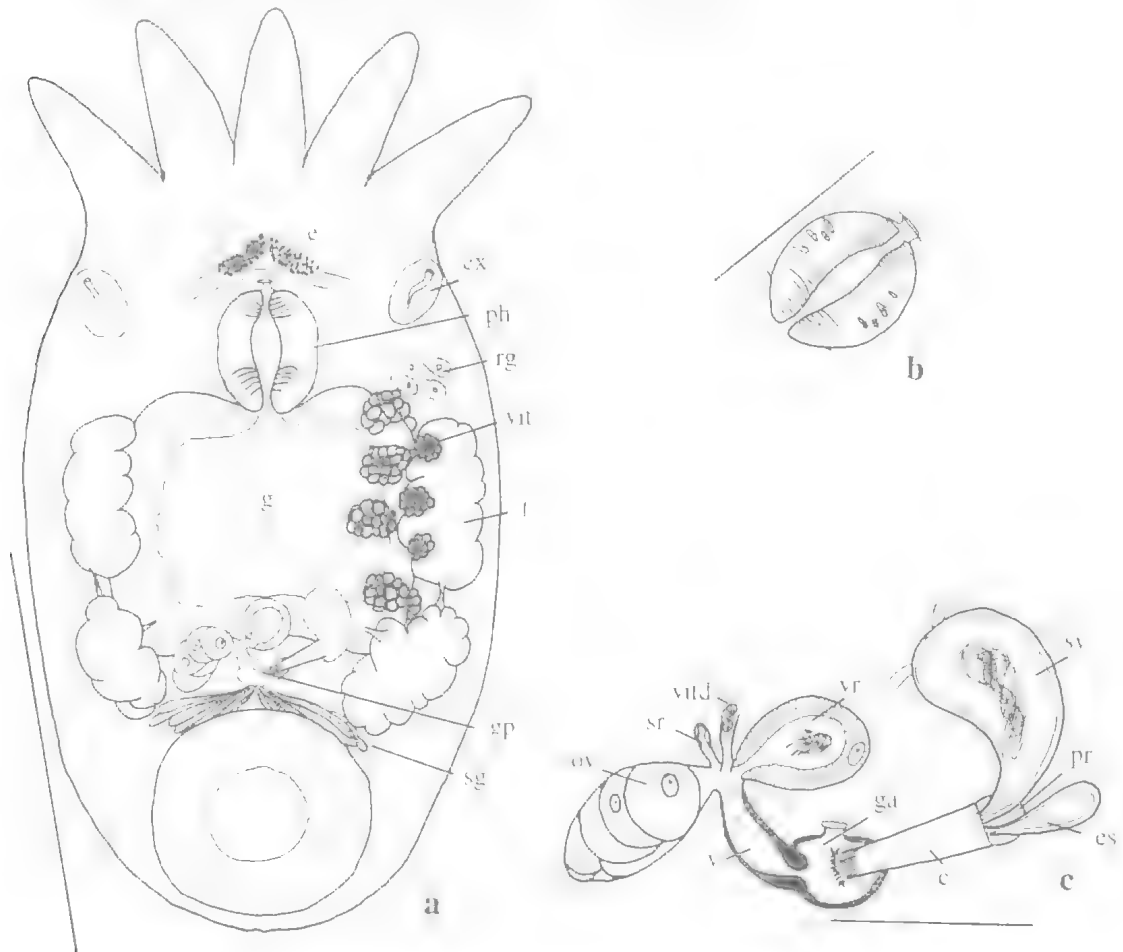


FIG. 4. *Temnocephala minuta* n.sp. a, internal anatomy of whole animal; b, pharynx; c, detail of reproductive system. Scales: a, 250 μ m; b, 100 μ m; c, 50 μ m.

DESCRIPTION

External characteristics. Body about 550 μm long, and 300 μm wide; rounded to oval or elliptical, dorso-ventrally compressed, but without flanges. Pigment confined to eyes. Posterior adhesive disc pedunculate: disc diameter 120 μm at rim, disc peduncle about 50 μm in diameter. Epidermis syncytial, about 2 μm high dorsally and ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ventrally, as wide as long, about 80 μm ; strong, undivided, with nucleated cells in muscle blocks; lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles not forming a crenulate buccal rim. Pharynx sphincters stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa. Gastrodermis about 20–30 μm high. Gut contains bacteria.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled, about 30 μm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Eyes present, contiguous, 25 \times 15 μm . Eye pigment granules irregular, mostly small, red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes, few <10 each side; 12–15 μm in diameter, with inconspicuous rhabdite tracts. Rhabdites apparently only accumulate on tentacles. Oesophageal glands and ootype glands inconspicuous (absent?). Shell glands present (a small cluster ventral to gonopore). Postero-lateral glands absent. Disc glands present.

Muscles. Longitudinal muscles of body wall stronger ventrally (especially at base of tentacles). Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles strong. Attachment muscles of pharynx weak. Attachment muscles of adhesive disc strong. Muscles controlling male organ weak.

Reproductive system ♀. Genital atrium small (but muscular). Genital complex scattered. Ovary about 30–50 μm in diameter. Vesicula resorbens present, about 25–30 μm across, 5 μm thick wall; lying free of gut wall, not open to gut. Seminal receptacle, single, 7 \times 3 μm . Vagina short, simple (but with sphincter at opening to genital atrium). Vitellaria clustered, laterally above and below testes.

Reproductive system ♂. Testes elliptical; anterior about 110 \times 66 μm , lobulate, lateral to gut, posterior about 100 \times 63 μm , lobulate, posterior

to gut. Vasa deferentia narrow. Seminal vesicle about 63 \times 40 μm . Ejaculatory sac present, with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft straight. Cirrus hardly tapering, 36 μm long, 11 μm wide at base. Cirrus introvert not swollen, 7 μm or 1/5 of the cirrus length. Cirrus spinelets minute, few rows, i.e. <20.

ETYMOLOGY

From *minutus* L. = small, refers to body size.

REMARKS

This species resembles most closely *T. cita* Hickman, 1967 in lacking pigment except for the eyes and in possession of a cirrus without a median spine. *T. cita* is very much larger, has a cirrus about 5 \times as big, 4 seminal receptacles (not one), and smooth, unequal testes (not subequal, lobed ones). The only other unpigmented species are *T. dendyi* Haswell, 1893 and *T. engaei* Haswell, 1893. Both these species have a median spine within the cirrus.

***Temnocephala neqae* n.sp.**
(Figs 5, 11f)

MATERIAL EXAMINED

HOLOTYPE, ex gills of *Macrobrachium rosenbergii* (Palaemonidae), Mitchell R. at Mt Carbine (16.32°S, 145.08°E), Nov. 1981, J. Short, Form./Hx, GL14518 (W).

PARATYPES: same data as holotype, GL14519 (W); ex gills of *M. rosenbergii* (Palaemonidae), Mitchell R., Dec. 1981, B. Power, Form./Mallory's GL14525–6 (LS[2,3]), Form./Gomori's GL14527 (TS[2]).

OTHER MATERIAL: same data as holotype, GL14520–35 (W); Form./H&E GL14537 (LS[3]); GL14538 (egg on gills of host); ex gills of *M. rosenbergii* (Palaemonidae), Mitchell R., Dec. 1981, B. Power, Form./Mallory's GL14536 (W).

DESCRIPTION

External characteristics. Body about 800–1400 μm (mean=1040 μm) long, and 430–720 μm (mean=540 μm) wide; oval or elliptical, dorso-ventrally compressed, with flanged edges. Pigment confined to eyes. Posterior adhesive disc pedunculate: disc diameter 220 μm at rim, disc peduncle about 125 μm across. Epidermis syncytial, 5 μm high dorsally, 3 μm high ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed ventrally, wider

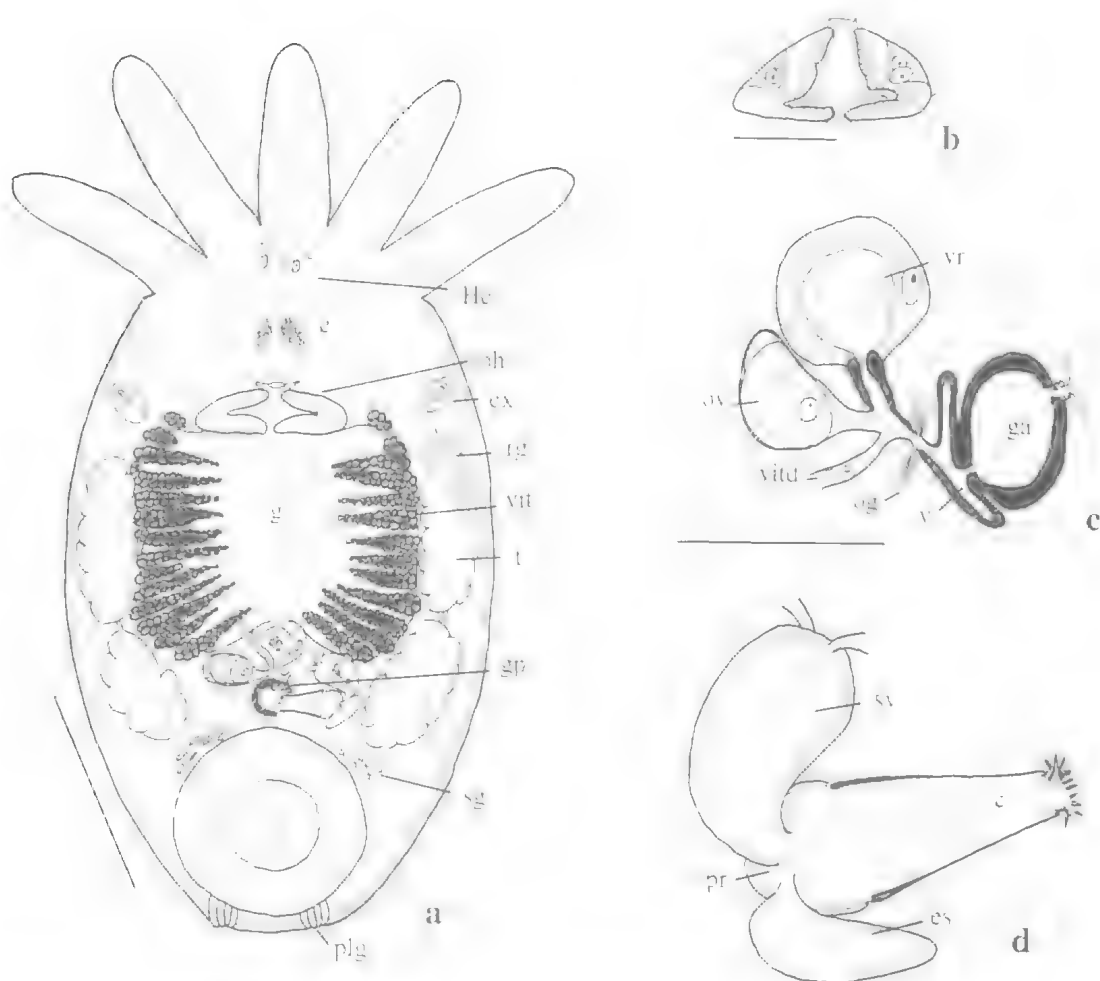


FIG. 5. *Temnocephala neqae* n.sp. a, internal anatomy of whole animal; b, pharynx; c, detail of female reproductive system; d, detail of male reproductive system. Scales: a, 250 μ m; b, 100 μ m; c-d, 50 μ m.

than long, about 95 \times 180 μ m; strong, undivided, with nucleated cells within muscle blocks; lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles forming a crenulate buccal rim. Pharynx sphincters stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa. Gastrodermis to 16 μ m high. Gut contains ?rotifers.

Excretory system. Excretory pores posterior to mouth. Excretory ampulla a simple vacuole, thick walled (12 μ m), about 50 \times 36 μ m. Major excretory ducts conspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, contiguous, about 40 \times 30 μ m. Eye pigment granules irregular, mostly small, black-brown.

Glands. Rhabdite glands in lateral fields anterior to anterior testes, numerous, 10 or more each side; about 20 μ m in diameter, with prominent rhabdite tracts to tentacles. Rhabdites only accumulate on tentacles (?). Haswell's cells inconspicuous (only two before brain), each ill defined about 80 \times 50 μ m. Oesophageal glands present. Ootype glands prominent. Shell glands in prominent lateral fields discharging to gonopore. Postero-lateral glands prominent. Disc glands present.

Muscles. Longitudinal muscles of body wall stronger ventrally, Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles and attachment muscles of pharynx weak. Attachment muscles of adhesive disc mod-

erately strong. Muscles controlling male organ strong.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium large, muscular. Genital complex scattered. Ovary about $62 \times 50 \mu\text{m}$. Vesicula resorbens present, about $48 \times 80 \mu\text{m}$, $13 \mu\text{m}$ thick wall; embedded in gut wall, opens to gut (in some). Seminal receptacles not present. Vaginal teeth absent. Vagina simple (muscular). Vitellaria dendritic, lateral. Egg capsules ellipsoid, about $300 \times 100 \mu\text{m}$; attached on end on a stalk, on gills.

Reproductive system ♂. Testes elliptical: anterior about $170 \times 85 \mu\text{m}$, lobulate, lateral to gut; posterior about $165 \times 95 \mu\text{m}$, lobulate, lateral to or posterior to gut. Vasa deferentia narrow, entering seminal vesicle separately. Seminal vesicle about $70 \times 30 \mu\text{m}$. Ejaculatory sac present, with narrowed neck. Prostate bulb separate, i.e. wider than cirrus base. Cirrus shaft straight. Cirrus hardly tapering, $52 \mu\text{m}$ long, $30 \mu\text{m}$ wide at base. Cirrus introvert not swollen, only about $12 \mu\text{m}$ or $1/4$ of the cirrus length, i.e. about the length of the 2-3 rows of cirral spines. Cirrus spinelets moderately sized, few rows, i.e. <20 .

ETYMOLOGY

The specific name refers to northeast Queensland.

REMARKS

The only described species with prominent postero-lateral glands is *Temnocephala chaeropsis* Hett, 1925 from a crayfish '*Chaerops preissi*' from near Mammoth Cave, WA. Unlike the present species, the glands are very close together; among other differences *T. chaeropsis* is much bigger, has four seminal receptacles, evidently lacks an ejaculatory sac and the introvert of the cirrus is more elaborate. Both *T. athertonensis* and *T. butlerae* (see above) also have postero-lateral glands; in neither species are they prominent and easily seen; furthermore, both species are pigmented, unlike the present species.

Temnocephala queenslandensis n.sp.

(Fig. 6)

MATERIAL EXAMINED

HOLOTYPE: ex *Macrobrachium australiense* (Palaemonidae), Hayes Ck off Moggill Ck Brisbane ($27.30.4^{\circ}\text{S}$, $152.55.8^{\circ}\text{E}$), 7 Mar. 1990, L. Cannon & K. Sewell, AFA/Haemalum GL14539 (W).

PARATYPES: same data as holotype, AFA/H&E GL14540-1 (LS[1,1]).

OTHER MATERIAL: ex *M. australiense* (Palaemoni-

dae), Highvale (27.23°S , 152.48°E), 10 May 1990, L. Cannon & K. Sewell, Bouin's/H&E GL14542 (LS[1]); AFA/Haemalum GL14543 (W); Upper Cedar Ck ($27.19.2^{\circ}\text{S}$, $152.55.8^{\circ}\text{E}$), 10 Apr. 1990, L. Cannon & K. Sewell, Boiling water/AFA/Haemalum GL14544 (W); same data as holotype 14545-9 (W); Ithaca Ck, Brisbane (27.29°S , 152.57°E), 20 Oct. 1988, J. Short, Form./Hx GL14550 (W); Gold Ck, Brisbane ($27.25.6^{\circ}\text{S}$, $152.50.9^{\circ}\text{E}$), 6 Mar. 1990, L. Cannon & K. Sewell, AFA/Haemalum GL14551-2 (W); Bouin's/H&E GL14553-4 (FS[1,1]); Booloumba Ck (26.39°S , 152.39°E), 23 Mar. 1990, L. Cannon & K. Sewell, AFA/Haemalum GL14609-11 (W); AFA/H&E GL14612-5 (LS[1,1,1,1]); Six mile Ck, Cooran (26.20°S , 152.50°E), 23 Mar. 1990, L. Cannon & K. Sewell, SUSA/Haemalum GL14616 (W); SUSA/Haemalum GL14617-8 (LS[1,1]); AFA/Haemalum GL14619-21 (W); Bouin's/H&E GL14622-3 (W); Kin Kin Ck (26.16°S , 152.53°E), 23 Mar. 1990, L. Cannon & K. Sewell, Bouin's/Haemalum GL14624-5 (W); AFA/Haemalum GL14626-28 (W); AFA/H&E GL14629-30 (LS[2,1]); Bouin's/H&E GL14631 (LS[2]); Kroombit Ck, Kroombit Tops ($24.23.0^{\circ}\text{S}$, $151.00.2^{\circ}\text{E}$), 20 Sep. 1990, L. Cannon & K. Sewell, AFA/Hx GL14632 (W); AFA/H&E GL14633 (LS[1]); Tributary of Broken R., Eungella NP ($28.10.8^{\circ}\text{S}$, $148.32.2^{\circ}\text{E}$), 21 Sep. 1990, L. Cannon & K. Sewell, Hot water/AFA/Hx GL14634-5 (W); Bouin's/H&E GL14636-8 (LS[1,1,1]); Stuart Ck, Townsville ($19.19.4^{\circ}\text{S}$, $146.50.2^{\circ}\text{E}$), 23 Sep. 1990, L. Cannon & K. Sewell, AFA/Hx GL14639 (W); Bouin's/H&E GL14640 (LS[1]); upper Pozzle Ck, Hidden Valley, Paluma (18.59°S , 146.01°E), 2 May 1982, L. Winsor, Form./Hx GL14641 (W); Form./H&E GL14642-3 (LS[2,1]); tributary (No. 4) of Blackfellow Ck, Edmon-ton ($17.00.6^{\circ}\text{E}$, $145.43.0^{\circ}\text{E}$), 28 Sep. 1990, L. Cannon & K. Sewell, AFA/Hx GL14646 (W); Rocky Ck, Car-been ($17.11.2^{\circ}\text{S}$, $145.26.8^{\circ}\text{E}$), 28 Sep. 1990, L. Cannon & K. Sewell, Bouin's/H&E GL14647-8 (LS[1,1]); Jumrun Ck, Kuranda ($16.46.8^{\circ}\text{S}$, $145.38.0^{\circ}\text{E}$), 28 Sep. 1990, L. Cannon & K. Sewell, Hot water/AFA/Hx GL14649; Bouin's/H&E GL14650, 18241 (LS[1,2]); Western R., Cragg Family Bridge, Winton ($22.25.0^{\circ}\text{S}$, $143.01.9^{\circ}\text{E}$), 2 Oct. 1990, L. Cannon & K. Sewell, AFA/Hx GL18242 (W); Bouin's/H&E GL18243 (LS[1]); Longreach Waterhole, Longreach ($23.24.7^{\circ}\text{S}$, $144.13.8^{\circ}\text{E}$), 3 Oct. 1990, L. Cannon & K. Sewell, Bouin's/H&E GL18244-5 (LS[2,1]); Lagoon Ck, Bar-caldine ($23.33.5^{\circ}\text{S}$, $145.16.6^{\circ}\text{E}$), 23 Sep. 1990, S. Cook, Alcohol/Haemalum GL18246-48 (W); Dawson R., Taroom (25.39°S , 149.48°E), 3 Dec. 1986, L. Can-non & J. Jennings, AFA/Haemalum GL18249-50 (W); AFA/H&E GL18251 (LS[2]); Carnarvon Ck ($25.06.5^{\circ}\text{S}$, $148.18.3^{\circ}\text{E}$), 18 Sep. 1990, S. Cook, Alco-hol/Hx GL18252 (W); ex *M. tolmerum* (Palaemoni-

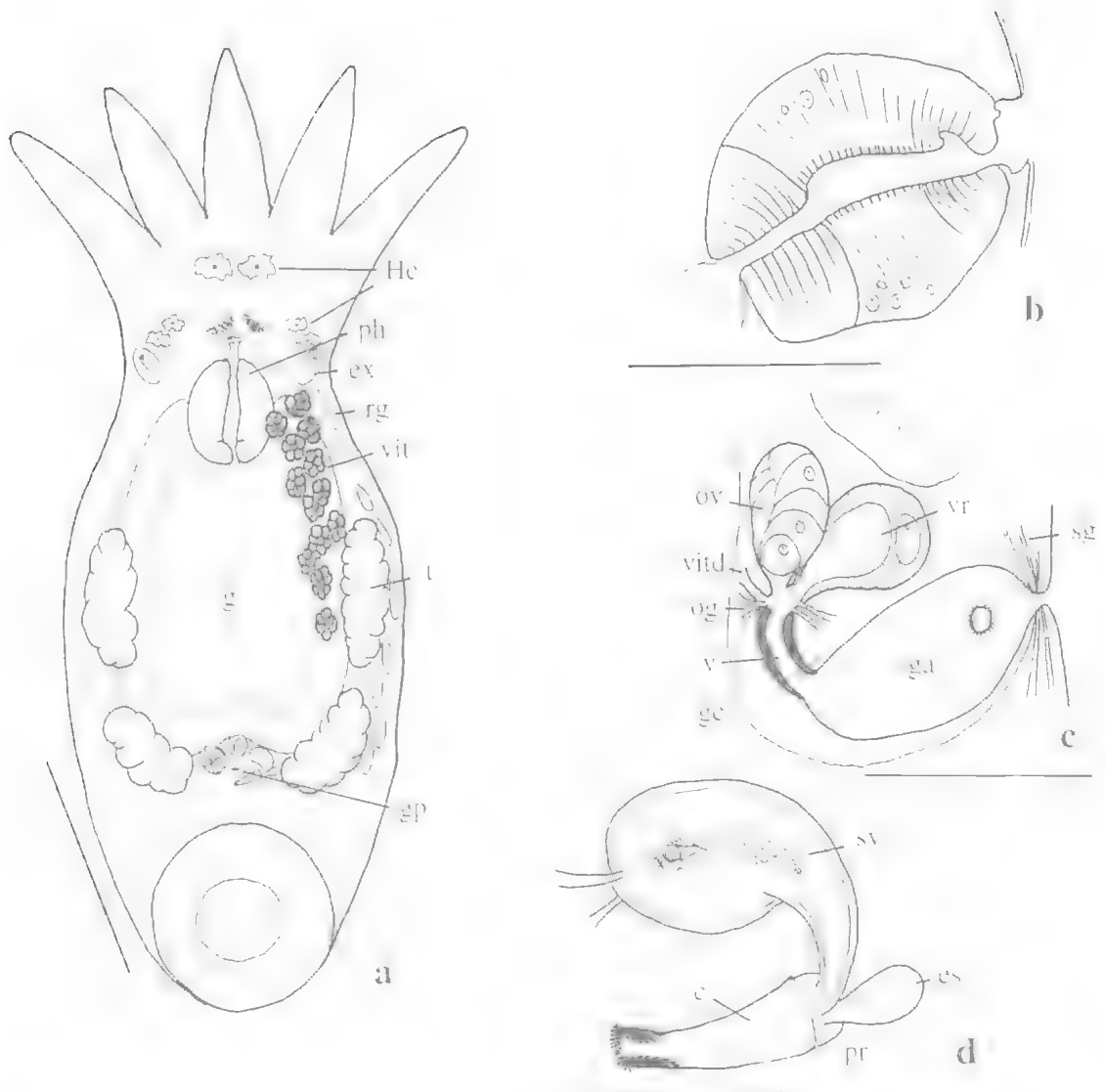


FIG. 6. *Termiocephala queenslandensis* n.sp. a, internal anatomy of whole animal; b, pharynx; c, detail of female reproductive system; d, detail of male reproductive system. Scales: a 250 μ m; c, 100 μ m; b, d, 50 μ m.

dae), Freshwater Ck, Cairns (16.54.1°S, 145.42.4°E), 23 Sep. 1990, L. Cannon & K. Sewell, AFA/Hx GL14644 (W); Bouin's/H&E GL14645 (LS[1]).

DESCRIPTION

External characteristics. Body about 650–950 μ m (mean=775 μ m) long, and 290–350 μ m (mean=315 μ m) wide; oval or elliptical, not dorso-ventrally compressed. Pigment confined to eyes. Posterior adhesive disc pedunculate: disc diameter 155 μ m at rim, disc peduncle about 70 μ m across. Epidermis syncitial (a strongly

staining basement membrane and numerous cell walls seen), 2 μ m high dorsally and ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous. Pharynx directed antero-ventrally, as wide as long, about 80 μ m in diameter; strong, not divided into anterior and posterior parts, without conspicuous nucleate cells within muscle blocks; lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles not forming an obvious crenulate buccal rim. Pharynx sphinc-

ters stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa. Gastrodermis 50 µm high.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled (10 µm), about 40 × 20 µm. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, contiguous, about 20 × 10 µm. Eye pigment granules medium, even sized, black-brown.

Glands. Rhabdite glands extending laterally beyond testes, numerous, 10 or more each side; 7-10 µm in diameter, with prominent rhabdite tracts to tentacles. Rhabdites only accumulate on tentacles. Haswell's cells present, 2 before eyes and two before each excretory ampulla. Oesophageal glands present. Ootype glands present. Shell glands in prominent lateral fields discharging to gonopore. Postero-lateral glands inconspicuous (absent?). Disc glands present.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles moderately strong. Attachment muscles of pharynx weak. Attachment muscles of adhesive disc strong (moderately). Muscles controlling male organ weak.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium commodious. Genital complex in weak capsule. Ovary about 115 × 40 µm. Vesicula resorbens present, about 40 µm in diameter, 8-10 µm thick wall; embedded in gut wall, opens to gut (in some). Seminal receptacles absent. Vagina short, simple. Vitellaria in lateral clusters.

Reproductive system ♂. Testes elliptical: anterior about 115 × 40 µm, lobulate, lateral to gut; posterior about 100 × 50 µm, lobulate, posterior to gut. Vasa deferentia swollen, entering seminal vesicle separately. Seminal vesicle about 50 × 20 µm. Ejaculatory sac present, but small with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base (not well defined). Cirrus shaft gently curved (proximally very fine). Cirrus hardly tapering, 45 µm long, 17 µm wide at base. Cirrus introvert not swollen (slightly thickened and noticeably more thickened than shaft), about 9 µm or nearly 1/5 of the cirrus length. Cirrus spinelets moderately sized, few rows, i.e. <20.

ETYMOLOGY

The specific name refers to the locality, Queensland.

REMARKS

Four species completely lack pigment except for the eyes, viz., *T. cita* Hickman, 1967, *T. dendyi* Haswell, 1893 *T. engaei* Haswell, 1893 and *T. minuta* (see above). Only *T. cita* and *T. minuta* have a cirrus without a median spine, but the cirrus is much larger (3-4 ×) in *T. cita*, and is slightly smaller and straighter in *T. minuta*, than in the present species. *T. cita* also has smooth, oval testes of unequal size and possesses 4 seminal receptacles, whereas *T. minuta* has a single seminal receptacle. These characters distinguish these worms from *T. queenslandensis*.

Temnocephala sp.

MATERIAL EXAMINED

ex shrimp (Atyidae), Sandy Ck nr Taroom (25.39°S, 149.48°E), 3 Dec. 1986, L. Cannon & J. Jennings, Form./Haemalum., GL14517 (W).

DESCRIPTION

External characteristics. Body about 315 µm long, and 200 µm wide; rounded, dorso-ventrally compressed, but without flanges. Pigment entirely absent, i.e. not even eyes. Posterior adhesive disc pedunculate: disc diameter 100 µm at rim, disc peduncle about 60 µm across. Epidermis syncytial (?). Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ventrally, wider than long, about 56 × 42 µm; strong, undivided, without prominent nucleate cells in muscle blocks; lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles forming a slightly crenulate buccal rim. Pharynx sphincters stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa.

Excretory system. Excretory pores dorso-lateral, lateral to mouth. Excretory ampullae about 40 × 35 µm, thick walled (about 5 µm). Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain bilobed. Major nerve trunks inconspicuous. Eyes absent.

Glands. Rhabdite glands lateral to testes; with inconspicuous rhabdite tracts.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally.

Reproductive system ♀. Gonopore mid-ven-

tral, in posterior third of body. Genital atrium small (but muscular). Genital complex scattered. Ovary about $18 \times 10 \mu\text{m}$. Vesicula resorbens present, about $31 \times 21 \mu\text{m}$; lying free of gut wall. Seminal receptacles not present (?). Vagina short, simple. Vitellaria dendritic.

Reproductive system ♂. Testes elliptical: anterior about $70 \times 35 \mu\text{m}$, lobulate, lateral to gut, posterior about $35 \times 40 \mu\text{m}$, lobulate, posterior to gut. Vasa deferentia swollen. Seminal vesicle about $35 \times 18 \mu\text{m}$. Ejaculatory sac present. Cirrus shaft gently curved. Cirrus hardly tapering, $36 \mu\text{m}$ long, $14 \mu\text{m}$ wide at base. Cirrus introvert not swollen, about $9 \mu\text{m}$ or $1/4$ of the cirrus length. Cirrus spinelets minute, few rows, i.e. <20 .

REMARKS

As this is a single immature specimen no type designation is made. The complete lack of eyes, however, strongly suggests this will prove a new species.

Temnohaswellia Pereira & Cuocolo, 1941

Generic diagnosis. Temnocephalidae with 6

anterior tentacles, a posterior adhesive disc, two pairs of testes postero-lateral to gut.

Temnohaswellia pugna n.sp. (Figs 7, 11g)

MATERIAL EXAMINED

HOLOTYPE: ex *Caridina* sp. (?nilotica) (Atyidae), Aplin Weir on Ross R., Townsville (19.22°S , 146.44°E), 1976, L. Winsor, Form./Picrocarmine GL14579 (W).

DESCRIPTION

External characteristics. Body about $1700 \mu\text{m}$ long (tentacles about $500 \mu\text{m}$), and $1000 \mu\text{m}$ wide; rounded, dorso-ventrally compressed, with flanged edges. Pigment confined to eyes and adjacent area (just a scatter between eyes). Posterior adhesive disc pedunculate: disc diameter $350 \mu\text{m}$ at rim, disc peduncle about $180 \mu\text{m}$ across. Disc musculature does not create surface ridges. Epidermis syncytial (?). Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ven-

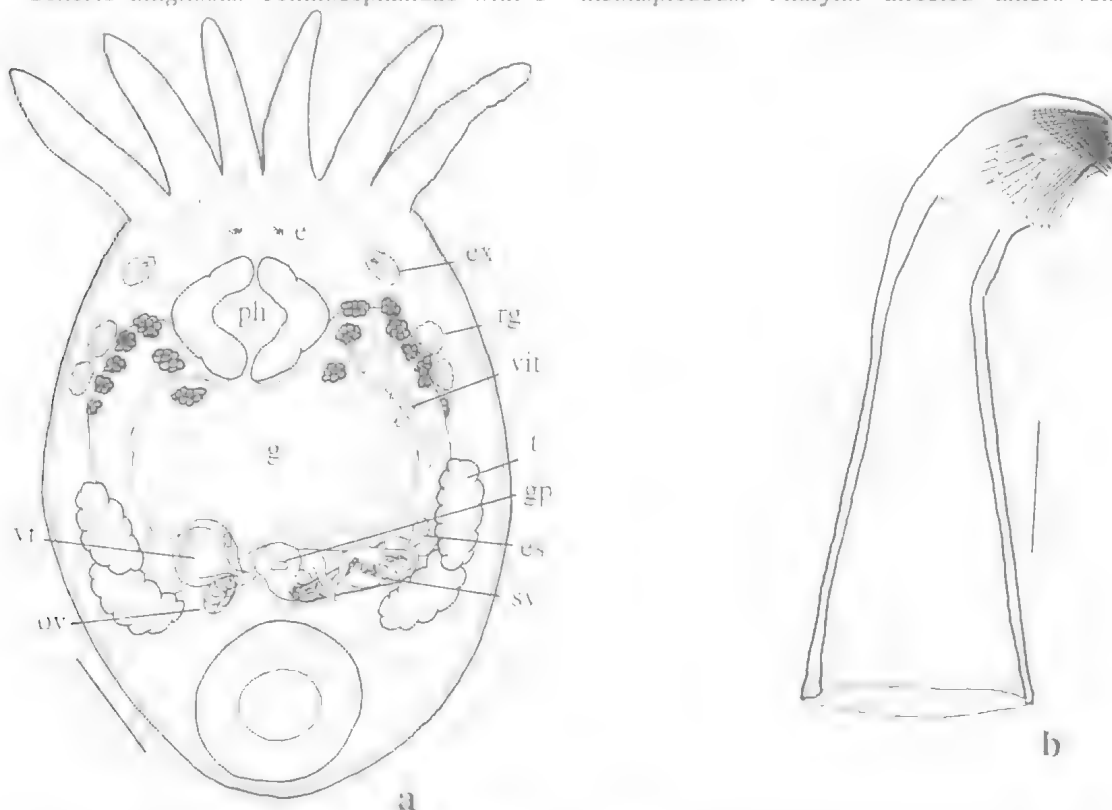


FIG. 7. *Temnohaswellia pugna* n.sp. a, internal anatomy of whole animal; b, cirrus. Scales: a, $250 \mu\text{m}$; b, $50 \mu\text{m}$.

trally, wider than long, about $360 \times 270 \mu\text{m}$; strong, undivided, with nucleate cells within muscle blocks; lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles forming a crenulate buccal rim. Pharynx sphincters subequal, slightly stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, with 3 ill-defined septa per side. Gastrodermis about $80 \mu\text{m}$ high. Gut contains muscle, crustacea and diatoms.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla strongly coiled, thin walled ($10 \mu\text{m}$), about $90 \times 70 \mu\text{m}$. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, discrete, well separated (but scattered granules between them), about $20 \mu\text{m}$ across. Eye pigment granules irregular, mostly small, black-brown.

Glands. Rhabdite glands? in lateral fields anterior to anterior testes, in two clumps (the smaller is posterior), with prominent rhabdite tracts to tentacles. Rhabdites evident in dorsal and ventral epidermis. Haswell's cells inconspicuous (absent?). Postero-lateral glands absent.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium small. Genital complex scattered. Ovary about $70 \times 5 \mu\text{m}$. Vesicula resorbens present, about $140 \mu\text{m}$ across, $15 \mu\text{m}$ thick wall; lying free of gut wall, not open to gut. Seminal receptacles absent (?). It is not clear from the specimen if vaginal teeth or muscular ribs are present. Vagina complex, outer region muscular, inner simpler. Vitellaria dendritic, dorsal over gut and lateral (plus some ventral behind pharynx).

Reproductive system ♂. Testes elliptical: anterior about $250 \times 100 \mu\text{m}$, posterior about $220 \times 100 \mu\text{m}$, lobulate, slightly overlapping. Vasa deferentia swollen. Seminal vesicle sinuous about same length as cirrus. Ejaculatory sac present, with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft straight. Cirrus strongly tapering, $240 \mu\text{m}$ long, $90 \mu\text{m}$ wide at base. Cirrus introvert swollen, slightly thickened and reflexed as with a clenched fist, about $80 \times 45 \mu\text{m}$ or $1/3$ of the cirrus length. Cirrus spines apparently at base of introvert. Cirrus spinelets minute to moderately sized, numerous rows, i.e. >20 .

ETYMOLOGY

From *pugnus* L. = fist, referring to the shape of the cirrus introvert.

REMARKS

Pereira & Cuocolo (1941) erected the genus *Temnohaswellia* with *T. novaezealandiae* (Haswell, 1888) as the type species. They included in the genus *T. comes* (Haswell, 1893) and placed the poorly described *T. simulator* (Haswell, 1924) in synonymy with it. Baer (1953) rejected the genus believing the possession of 6 tentacles insufficient justification on which to erect a new genus, although he allowed that coupled with the vaginal teeth found in *T. novaezealandiae* there may be justification. This latter character is, however, absent from *T. comes*.

First, Haswell (1924) who was a careful worker clearly distinguished *T. simulator* from *T. comes*: *T. simulator* is here recognised as a valid species. Secondly, Haswell (on the same page) suggests the elaborate vagina of *T. novaezealandiae* may be 'an enormous extension of the thick sphincter of *T. comes* and the metraterm which subtends it.' Thus Haswell clearly saw a link between these species. Further, the relatively posterior position of the testes (overlapping and at the rear of the gut) and the presence of two pairs of clumped glands at the anterior lateral margin of the gut as Fyfe (1942) showed in *T. novaezealandiae* I believe provide characters coupled with the others to indicate these species are related. Fyfe (1942) claimed these paired anterior glands were prostate glands: their position certainly is in more keeping with rhabdite glands. The material available is not adequate to distinguish this character, and regrettably Haswell (1893) did not fully describe *T. comes*. Nevertheless, I believe the genus *Temnohaswellia* Pereira & Cuocolo, 1941 should be recognised as valid. Of the three known species, viz. *T. comes* (Haswell, 1893) which is unpigmented, and *T. simulator* (Haswell, 1924) and *T. novaezealandiae* (Haswell, 1888) which are pigmented, the present species more closely resembles *T. comes*, but may be distinguished by the cirrus which, though possessing a distinctive introvert, is not curved as in *T. comes*.

Temnohaswellia tetrica n.sp. (Fig. 8)

MATERIAL EXAMINED

HOLOTYPE: ex *Caridina* sp. (?nilotica) (Atyidae), Aplin Weir on Ross R., Townsville (19.22°S , 146.44°E), 1976, L. Winsor, Form./Picrocarmine GL14580 (W).

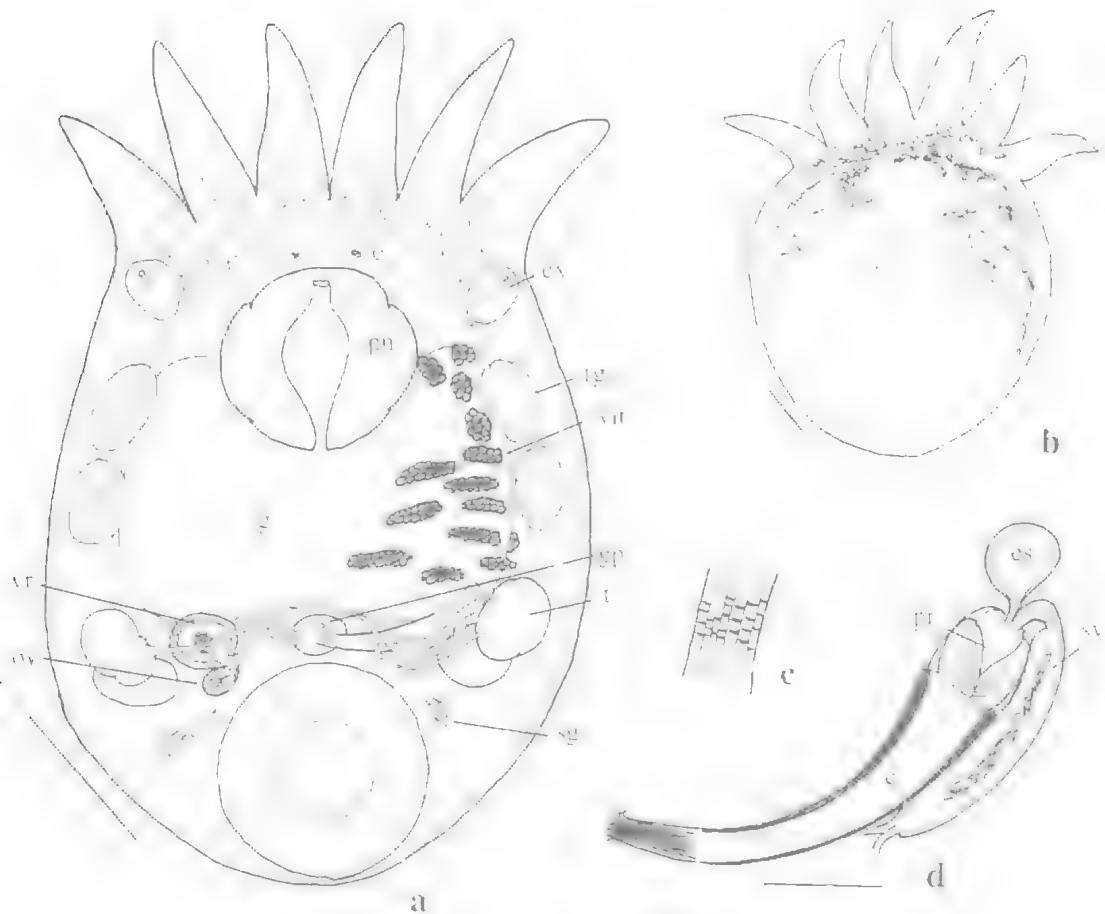


FIG. 8. *Temnohaswellia tetrica* n.sp. a, internal anatomy of whole animal; b, dorsal pigment pattern; c, detail of vaginal teeth; d, detail of male reproductive system. Scales: a,b, 250µm; c, not to scale; d, 100µm.

DESCRIPTION

External characteristics. Body about 2mm long (tentacles about 500µm), and 13mm wide; rounded, dorso-ventrally compressed, with flanged edges. Pigment a tracery over most of anterior dorsal surface. Posterior adhesive disc pedunculate; disc diameter 500µm at rim, disc peduncle about 250µm across. Epidermis syncytial (?). Cilia entirely absent (?).

Alimentary system. Mouth mid-ventral in anterior quarter of body, Buccal cavity or prepharynx conspicuous. Pharynx directed antero-ventrally, as wide as long, about 485µm across; strong, undivided, with nucleate cells within muscle blocks (?); lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles forming a crenulate buccal rim. Pharynx sphincters equal (?). Oesophagus inconspicuous. Gut lacking col-

our, wider than long; without septa. Gut contains diatoms.

Excretory system. Excretory pores anterior to mouth. Excretory ampulla a simple vacuole, thick walled, about 180µm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Eyes adjacent, about 30µm across, linked with a pigment mesh forming a single dark region. Eye pigment granules irregular, mostly small, black-brown.

Glands. Rhabdite glands? in lateral fields anterior to anterior testes (in two tandem clumps), individual gland cells within these clumps are not readily distinguishable; clumps 140-170 × 120 µm. With prominent rhabdite tracts to tentacles; rhabdites only accumulate on tentacles (?). Haswell's cells, oesophageal glands and ootype glands inconspicuous (absent?). Shell glands in

prominent lateral fields. Postero-lateral glands absent.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium small. Genital complex scattered. Ovary about 80 µm in diameter. Vesicula resorbens present, about 120 µm across; lying free of gut wall, not open to gut. Seminal receptacles absent (?). Vaginal teeth present, about 5 or 6 rows of fine scale-like teeth in columns. Vagina long, compartmentalised. Vitellaria dendritic, dorsal to ventral.

Reproductive system ♂. Testes rounded, smooth, about 175 µm in diameter, both posterior to the gut and slightly overlapping one another (the posterior more dorsal pair vacuolated and apparently invaded by nematodes). Vasa deferentia narrow (?), entering seminal vesicle separately. Seminal vesicle about 35 × 200 µm. Ejaculatory sac present, with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft curved. Cirrus hardly tapering, 350 µm long, 70 µm wide at base. Cirrus introvert not swollen, about 70 µm or 1/5 of the cirrus length. Cirrus spinelets moderately sized, numerous rows, i.e. >20.

ETYMOLOGY

From *tetricus* L. = forbidding, refers to the *vagina dentata*.

REMARKS

The presence of pigment indicates this species resembles *T. simulator* (Haswell, 1924) and *T. novaezealandiae* (Haswell, 1888). *T. novaezealandiae* is said to contain 'a system of formidable chitinous teeth' (Haswell, 1924) and thus, on that account, differs substantially from the present species which has only fine teeth. *T. simulator* also has papillae which 'assume the appearance of teeth', but in the present species there can be little doubt that teeth, not papillae, are present.

The cirrus of the present species is long, slender and curved, so resembles that of *T. novaezealandiae* according to Haswell (1893: pl. XIII, figs 17-18), but not according to Fyfe (1942) who, dealing with *T. novaezealandiae* with prominent vaginal teeth, illustrates and states that the cirrus (penis) is L-shaped. Details of *T. simulator* are sketchy; however, Haswell (1924) stated 'the entire reproductive system closely resembles that of *T. comes*': certainly the cirrus of *T. comes* is much less slender with a more pronounced introvert than occurs in the present species.

The presence of nematodes in the testes of the present species echoes a similar observation made by Haswell (1893) with regard to *T. comes* who said 'many of them had parasitic Nematodes or their eggs or embryos lodged in the testes'.

Achenella n. gen.

Type species. *Achenella sathonota* n.sp.

Generic diagnosis. Temnocephalidae with 5 anterior tentacles, a single pair of testes posterior to the gut, genital organs contained in a connective tissue capsule, vesicular resorbens posterior - not pushing up into or adjacent to the gut, a rosette organ (a cluster of single cells subtending a small disc embedded in the epidermis) anterior to the excretory ampulla, and vitellaria clustered along the lateral margins of the gut.

Species included in Achenella. *A. sathonota* n.sp., *A. cougal* n.sp.

Etymology. From *achen* L. = poor, impoverished; pertaining to having only one pair of testes. Temnocephalidae has several genera with two or more pairs of testes.

Achenella sathonota n.sp. (Figs 9, 12a-d, f-i)

MATERIAL EXAMINED

HOLOTYPE: ex *Caridina indistincta* (Atyidae), Gully nr Capalaba, Brisbane (27.32°S, 153.12°E), 22 Sep. 1988, L. Cannon, Bouin's/Hx GL14589 (W).

PARATYPE: ex *Caridina indistincta* (Atyidae), Water-hole on creek at Henderson Rd, Sheldon, Brisbane (27.36°S, 153.13°E), 18 Mar. 1990, L. Cannon, Bouin's/H&E GL14591 (LS[1]).

OTHER MATERIAL: Queensland - same data as holotype, H&E GL14597 (LS[1]); same data as paratype, AFA/Haemalum GL14594 (W); Bouin's/Mallory's GL14596 (LS[1]); ex *C. indistincta* (Atyidae), Trib. of Scrubby Ck, Sheldon, Brisbane (27.37°S, 153.05°E), 2 Oct. 1991, I. Olsson, Hot water Form./Hx GL14598 (W); GL14599-14600 (LS[2,2]), ex *C. indistincta* (Atyidae), stream nr Kin Kin (26.16°S, 152.53°E), 23 Mar. 1990, L. Cannon & K. Sewell, AFA/Haemalum GL14583 (W), GL14584-5 (W); AFA/H&E GL14586 (LS[1]), AFA/H&E GL14587-8 (LS[1,1]), ex 'shrimp' (? *C. indistincta*) (Atyidae), Daisy Hill, Brisbane (27.28°S, 153.01°E), 16 Apr. 1989, L. Cannon, Bouin's/Hx GL14590 (W); SUSA/Hx GL14592; AFA/Hx GL14593 (W); ex 'shrimp' (? *C. indistincta*) (Atyidae), Bulimba Ck (27.33°S, 153.07°E), 18 Jul. 1979, A. Arthington, Form./unstained GL14595; NSW - ex *Caridina macleodii*, tributary of Orara R., NSW (30.16.4°S, 153.03.1°E), 15 Feb. 1992, K. & S. Sewell,

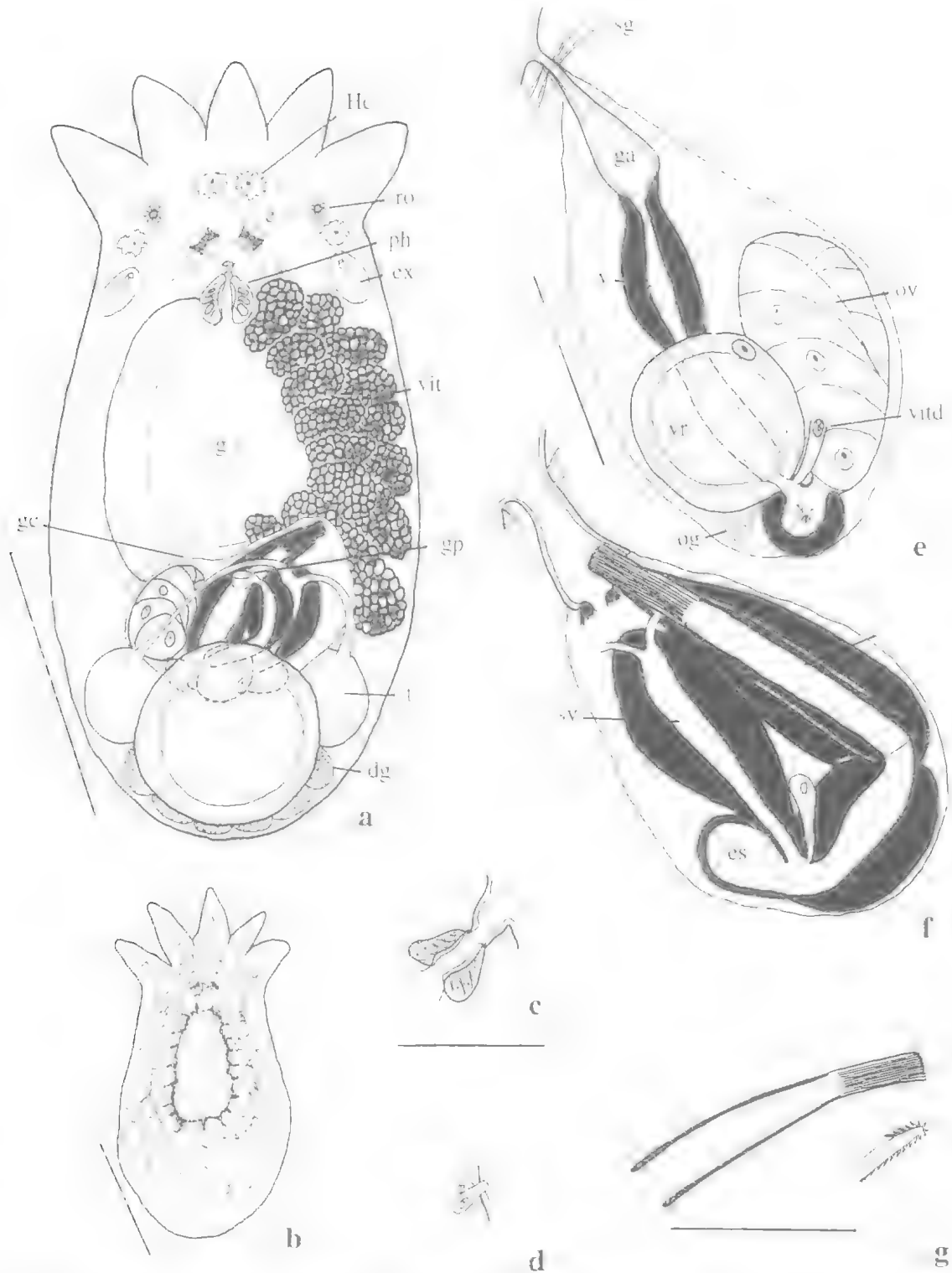


FIG. 9. *Achenella sathonota* n. gen., n.sp. a, internal anatomy of whole animal; b, dorsal pigment pattern; c, pharynx; d, rosette organ; e, detail female reproductive system; f, detail of male reproductive system; g, cirrus, and detail of spinelets. Scales: a, b, 250 μ m; c-d, e-f, g, 100 μ m.

Hot water Form./Haemalum GL14601 (W), GL14602 (W); Bouin's/H&E GL14603 (LS[1]), GL14606 (W); Bouin's/Hx GL14605, 14607 (W); Bouin's/H&E GL14608 (LS[1]).

DESCRIPTION

External characteristics. Body about 500-900 μm (mean=710 μm) long, and 250-380 μm (mean=330 μm) wide [specimens from NSW slightly larger, to 1200 μm long]; oval or elliptical, not dorso-ventrally compressed. Pigment extends to ventral surface (through parenchyma: especially dense about gut where it outlines the inner limits of the vitellaria). Posterior adhesive disc pedunculate: disc diameter 160 μm at rim, disc peduncle 120 μm across. Rosette organ about 50 μm anterior to excretory ampulla. Epidermis syncytial, 5 μm high dorsally, 9 μm high ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous. Pharynx directed antero-ventrally, as wide as long, about 50 μm across; very weak, undivided, with prominent cells within muscle blocks (though muscles barely discernible); lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles not forming an obvious crenulate buccal rim. Pharynx sphincters equal but very weak. Oesophagus inconspicuous. Gut lacking colour, wider than long; without septa. Gastrodermis 50 μm high. Gut contains eggs (of temnocephalan?), diatoms, cladocerans and nematodes.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled, about 50 \times 30 μm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks conspicuous ventrally. Eyes present, discrete, well separated (but joined by body pigment), about 20 μm across. Eye pigment granules medium, even sized (about 1.5 μm across), black-brown.

Glands. Rhabdite glands apparently a scatter of ventro-lateral glands about 20 μm in diameter, with inconspicuous rhabdite tracts. Rhabdites only accumulate on tentacles (?). Haswell's cells conspicuous, four (a pair before brain, another before excretory pores) about 20 μm across. Oesophageal glands inconspicuous (absent?). Oo-type glands present. Shell glands in prominent lateral fields discharging to gonopore. Posterior-lateral glands inconspicuous (absent?). Disc glands prominent, a discrete eosinophilic cluster.

Muscles. Longitudinal muscles of body wall of

equal size or strength dorsally and ventrally (and quite strong, about 3-4 μm wide). Circular muscles of body wall similar dorsally and ventrally (also 3-4 μm wide). Dorso-ventral muscles and attachment muscles of pharynx weak. Attachment muscles of adhesive disc strong. Muscles controlling male organ strong (about stylet and seminal vesicle and also strong as dorso-lateral bands extending antero-lateral and postero-lateral from the region of the gonopore).

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium commodious. Ovary to about 50 \times 90 μm . Vesicula resorbens present, about 50 \times 60 μm , 210 μm thick wall. Seminal receptacle single, hardly cut off from female canal. Vaginal teeth absent. Vagina long, compartmentalised (proximal region to about 75 μm long with muscle walls 4 μm thick, distal region to about 150 μm long with walls 25 μm thick). Vitellaria clumped, lateral (from excretory ampulla to testes - numerous large glands 75 μm across).

Reproductive system ♂. Testes rounded, about 80 μm in diameter, smooth. Vasa deferentia swollen, entering seminal vesicle separately. Seminal vesicle about 90 \times 60 μm , walls 20 μm thick. Ejaculatory sac present. Prostate bulb separate, i.e. wider than cirrus base. Cirrus shaft gently curved. Cirrus hardly tapering, 170 μm long, 25 μm wide at base. Cirrus introvert swollen, but only very little, about 45 μm or 1/4 of the cirrus length. Cirrus spines absent. Cirrus spinelets minute on a series of long sclerotic ridges, many rows i.e. >20.

ETYMOLOGY

From *sathon* Gr. = one with a large penis, referring to the relative size of the cirrus to body size.

REMARKS

Only one 5 tentacled species of temnocephalan has been described with one pair of testes, *Temnocephala brenesi* Jennings, 1968, from the shrimps, *Macrobrachium americanum*, in Costa Rica. The correct position of this species must await further study, but it does not appear to conform to *Achenella* n. gen.

In the present species the cirrus is slightly larger for specimens from Kin Kin and considerably larger (280 μm long and 55 μm wide at base) for those from *C. mccullochi* from NSW. This latter difference in size of the cirrus may reflect just bigger specimens or perhaps indicates these specimens from a different host and a distant

locality belong to a distinct species. Unless other differences become apparent all these specimens should be considered of the same species.

***Achenella cougal* n.sp.**
(Fig. 10)

MATERIAL EXAMINED

HOLOTYPE: ex *Paratya australiensis* (Atyidae), Upper Currumbin Ck, Gold Coast (28.14.6°S, 153.20.8°E), 12 Apr. 1991, L. Cannon & K. Sewell, Hot water Form./H&E GL14581 (LS[2]).

OTHER MATERIAL: same data as holotype, Hx GL14582 (damaged W).

DESCRIPTION

External characteristics. Body about 950µm long, and 400µm wide; oval or elliptical, not dorso-ventrally compressed. Pigment confined to eyes. Posterior adhesive disc broadly pedunculate: disc diameter 180µm at rim. Rosette organ about 100µm anterior to excretory pores. Epidermis syncytial about 5µm high dorsally and ventrally. Cilia entirely absent.

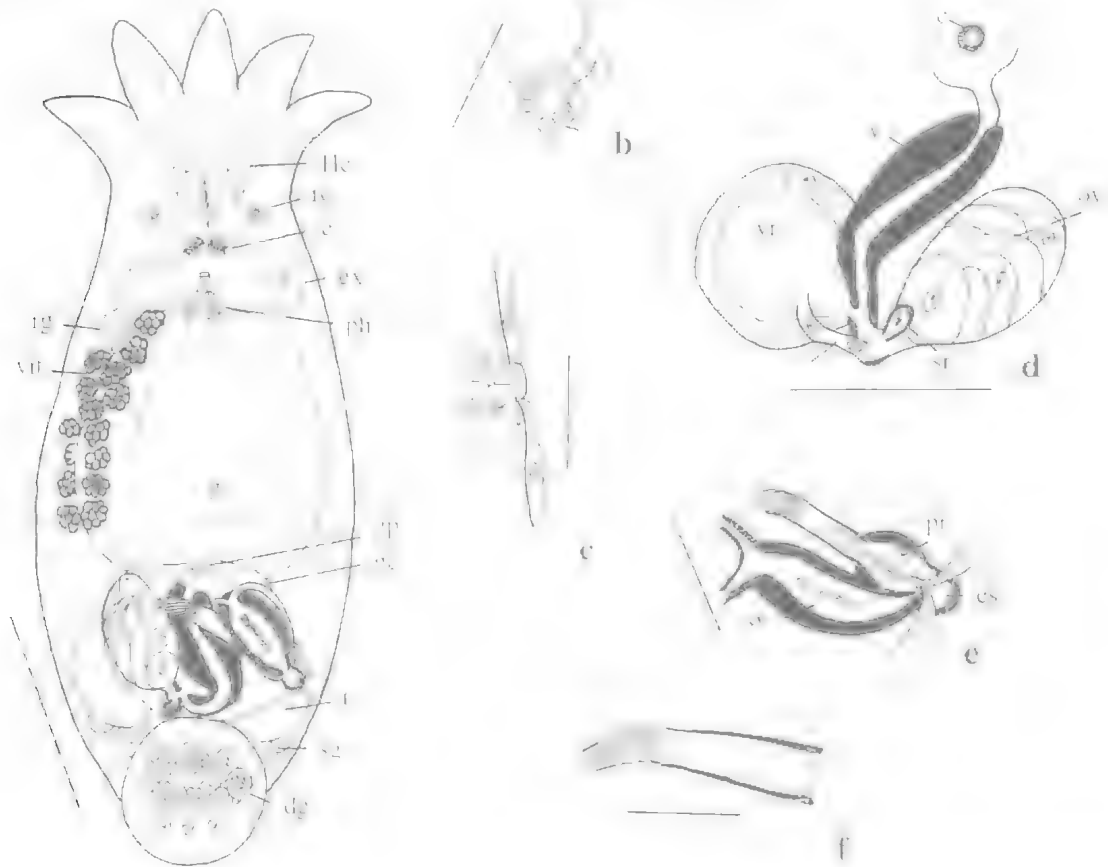
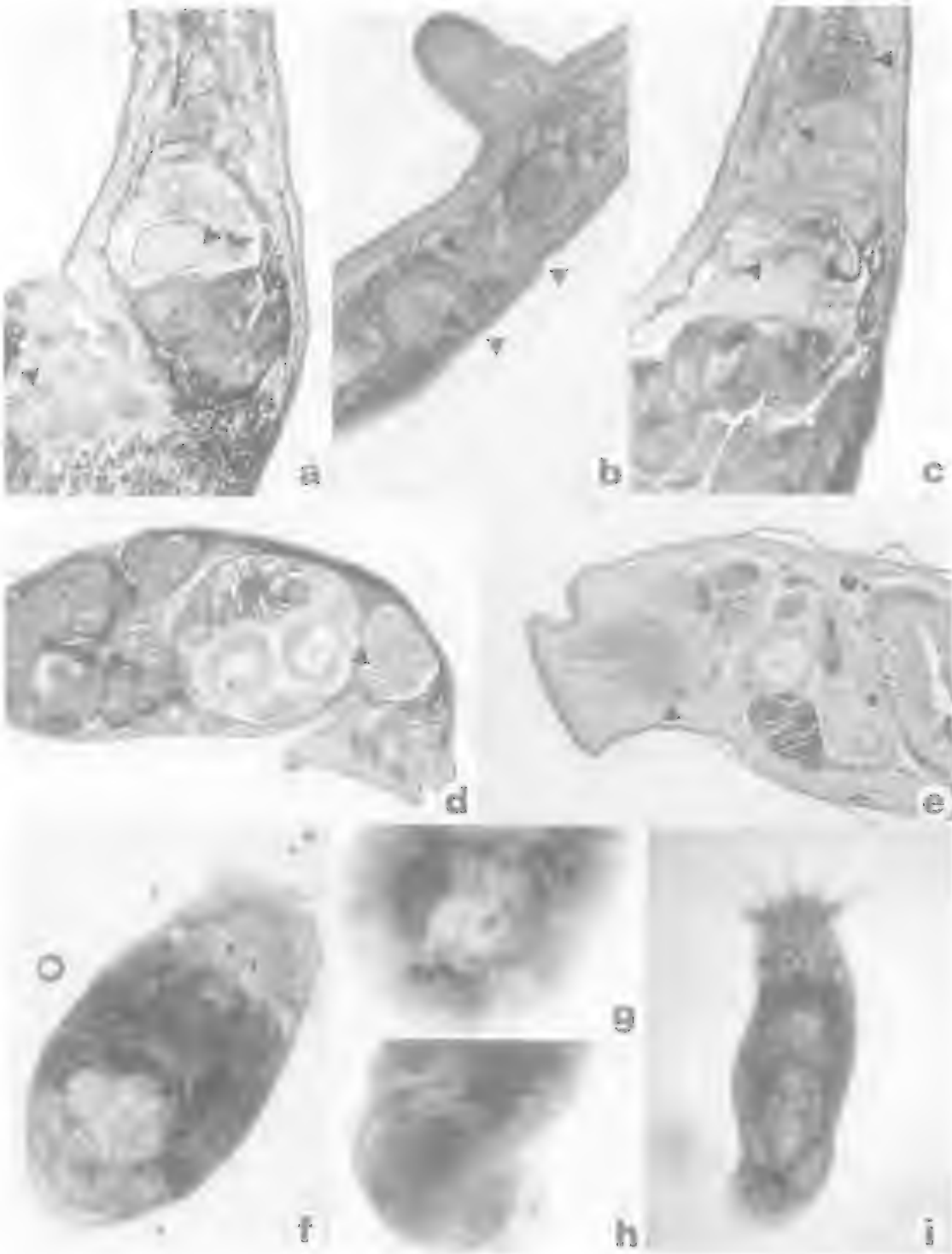


FIG. 10. *Achenella cougal* n.sp. a, internal anatomy of whole animal; b, pharynx; c, rosette organ; d, detail female reproductive system; e, detail of male reproductive system; f, cirrus. Scales: a, 250µm; b, 100µm; c, 50µm; d-e, 100µm; f, 50µm.

FIG. 11. Photomicrographs of new temnocephalans from crabs and shrimps. a-c, *Temnocephala athertonensis* n.sp.: a, pharynx showing prominent cells between sphincter blocks; b, genital capsule; c, weak postero-lateral glands; d, *Temnocephala butlerae* n.sp. genital region showing prominent ejaculatory sac; e, *Temnocephala improcera* n.sp. showing simple muscular pharynx: note pigment below body wall; f, *Temnocephala neqae* n.sp. posterior end showing prominent postero-lateral glands; g, *Temnohaswellia pugna* n.sp. cirrus; h, *Temnohaswellia tetrica* n.sp. showing shaft of cirrus and vaginal teeth, overlaying the introvert. Scales: 1cm = 100µm (a,b,e,g,h); 1cm = 50µm (c,d,f). Nomarski f,g,h.





Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous (muscular, about $50\mu\text{m}$ deep). Pharynx directed antero-ventrally, as wide as long, about $72\mu\text{m}$ in diameter; weak, undivided, with prominent cells within muscle blocks; lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles not forming an obvious crenulate buccal rim. Pharynx sphincters equal (very little musculature). Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa. Gastrodermis about $70\mu\text{m}$ high.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled ($12\text{--}15\mu\text{m}$), about $50\mu\text{m}$ in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain bilobed (with large bilobed forebrain). Eyes present, discrete, well separated, about $30\text{--}40\mu\text{m}$ across. Eye pigment granules medium, even sized, about $2\mu\text{m}$, black-brown to red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes (and anterior and lateral to pharynx), few, less than 10 each side; $15\text{--}25\mu\text{m}$ in diameter, with rhabdite tracts to base of tentacles. Rhabdites only accumulate on tentacles. Haswell's cells conspicuous, two together before forebrain, about $70\times 30\mu\text{m}$. Oesophageal glands and ootype glands inconspicuous (absent?). Shell glands present postero-lateral to testes open to gonopore. Postero-lateral glands absent. Disc glands prominent, scattered around testes with a cluster of deeply eosinophilic club shaped cisternae opening on to disc.

Muscles. Longitudinal muscles of body wall stronger ventrally. Dorso-ventral muscles and attachment muscles of pharynx weak. Attachment muscles of adhesive disc and muscles controlling male organ strong.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium large. Ovary about $130\times 80\mu\text{m}$. Vesicula resorbens present, about $90\mu\text{m}$ across, $15\mu\text{m}$ thick wall. Seminal receptacle single, about $20\mu\text{m}$ across. Vaginal teeth absent. Vagina long, compartmentalised, distally muscular $145\mu\text{m}$ long walls $25\mu\text{m}$ thick, proximally $40\mu\text{m}$ long walls $7\text{--}8\mu\text{m}$ thick. Vitellaria discrete (scattered), lateral about $20\mu\text{m}$ across.

Reproductive system ♂. Testes a single pair, rounded, about $140\mu\text{m}$ in diameter, smooth, posterior to gut. Vasa deferentia swollen (to about $20\mu\text{m}$), entering seminal vesicle separately. Seminal vesicle about $100\times 70\mu\text{m}$ with thick ($10\mu\text{m}$) walls. Ejaculatory sac present about $50\mu\text{m}$ in diameter, with wide neck (joins directly to back of prostate bulb). In holotype a very large prostate gland ($110\text{--}125\mu\text{m}$ across) lies anterior to testes. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft straight. Cirrus hardly tapering, $100\mu\text{m}$ long, $20\mu\text{m}$ wide at base. Cirrus introvert not swollen, about $40\mu\text{m}$ long tapering to $10\mu\text{m}$ wide; $1/3$ of the cirrus length. Cirrus spines present, on about 20 strong ribs spiralling out.

ETYMOLOGY

The specific name refers to the name of the locality. Currumbin Ck rises in Cougal National Park.

REMARKS

The lack of pigment in the body and the much smaller, more gracile cirrus serve to clearly distinguish this species from the only other member of the genus *A. sathonota*.

Achenella sp.

MATERIAL EXAMINED

2x *Austratya striolata* (Austratyidae), Yuccabine Ck, Kurrumba (18.13°S, 145.45°E), 10 Jul. 1985, R. Smith, (coll. no. 100137753).

DESCRIPTION

External characteristics. Body about $500\mu\text{m}$ long, and $400\mu\text{m}$ wide; oval or elliptical, not dorso-ventrally compressed. Pigment confined to eyes. Posterior adhesive disc pedunculate: disc diameter $140\mu\text{m}$ at rim, disc peduncle about $90\mu\text{m}$ across. Epidermis about $7\mu\text{m}$ high dorsally and ventrally. Cilia entirely absent (?).

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ventrally (?), as wide as long, about $70\mu\text{m}$ in diameter; weak, with nucleate cells within muscle blocks (?); without a conspicuous non-cellular lining.

FIG. 12. Photomicrographs of new temnocephalans from crabs and shrimps. a-d,f-i, *Achenella sathonota* n. gen., n.sp. a, weak pharynx, brain and eye; b, excretory pore and anterior to it the rosette organ; c, brain, forebrain and Haswell's cell; d, genital capsule and posterior testis; e, *Achenella cougal* n.sp. genital capsule and prominent cisternae of disc glands with a weakly pedunculate adhesive disc; f, specimen from Capalaba; g, posterior showing cirrus, specimen from Stretton; h, posterior (lateral) showing cirrus, specimen from Kin Kin; i, specimen from Orara R., NSW. Scales: 1cm = $50\mu\text{m}$ (a-c); 1cm = $100\mu\text{m}$ (d,e,g,f); 1cm = $250\mu\text{m}$ (f,i).

Pharynx sphincters equal (?). Gut lacking colour, as wide as long (?). Gastrodermis about 40 µm high.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled (20 µm), about 35–40 µm across. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, discrete, well separated, about 25 × 20 µm. Eye pigment granules medium, even sized, red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes (?); about 15 µm across. Shell glands present. Disc glands prominent, a discrete cluster.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles weak; attachment muscles of pharynx and of adhesive disc weak. Muscles controlling male organ strong, about 25 µm thick.

Reproductive system ♀. Gonopore mid-ventral, in posterior quarter of body. Genital atrium commodious. Ovary about 50 × 70 µm. Vesicula resorbens present, about 75 µm in diameter, about 20 µm thick wall. Vagina chambered and strongly muscular. Egg capsules ovoid or pyriform, about 225 µm in diameter; attached on side without stalk, on cephalothorax (inside branchial chamber).

Reproductive system ♂. Testes rounded. Seminal vesicle about 50 µm across. Ejaculatory sac present, with narrowed neck? Cirrus shaft straight. Cirrus hardly tapering, 100 µm long, 32 µm wide at base. Cirrus introvert not swollen, about 10 µm long or 1/9 of cirrus. Cirrus spinelets minute, few rows, i.e. <20.

REMARKS

This one sectioned specimen is tentatively placed in *Achenella* as there appears but one pair of testes, the genital organs are in a capsule and disc glands are prominent. Until better material is available it is not appropriate to provide a specific name.

ACKNOWLEDGEMENTS

I wish to acknowledge the generous support of the Australian Biological Resources Survey and the considerable help in the field from Mr Kim Sewell. For help in the laboratory I am indebted

to Lucille Gillespie and especially Christine Lee. John Short provided confirmation of identification of the various hosts. Thanks are also extended to Leigh Winsor, James Cook University, and Stephen Cook, Queensland Museum for some specimens.

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NOTES ON *PARMULARIA* MACGILLIVRAY (BRYOZOA: CHEILOSTOMIDA) FROM AUSTRALIA

P.J. CHIMONIDES AND P.L. COOK

Chimonides, P.J. & Cook, P.L. 1993 06 30: Notes on *Parmularia* MacGillivray (Bryozoa: Cheilostomida) from Australia. *Memoirs of the Queensland Museum* 33(1): 41-48. Brisbane. ISSN 0079-8835.

Colonies of *Parmularia* form leaf-like lobes, anchored above the surface of particulate sea-bottoms by a wide, turgid, extrazoidial rhizoid system. In spite of this distinctive colony form, species generally show striking similarities with those of two normally encrusting genera, *Emballothecha* Levinsen and *Calypsothecha* Harmer, and all three genera are here included in the family Parmulariidae Canu & Bassler. Four species, *P. obliqua* (MacGillivray), *P. quadlingi* (Haswell), *P. arnoldi* sp.nov. and *P. occidenta* sp.nov. are described. □ Bryozoa, *Parmularia*, Cheilostomida, Parmulariidae, *Emballothecha*, *Calypsothecha*, new species.

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Parmularia was introduced by MacGillivray (1887) who quoted a manuscript name mentioned in correspondence by George Busk. The distinctive leaf-like colonies, with large rhizoid systems, which support them above the surface of the substratum, are well-known in Recent Australasian bryozoan sand-faunas; fragments of colonies frequently occur in fossil assemblages from the Tertiary of Victoria. Living specimens have been described by Maplestone (1910), Bock (1982) and Cook & Chimonides (1985), all of whom particularly noted the brilliant red and orange pigments of embryos and coelomic tissues. Recognition of the genus is relatively easy, even from fragmented specimens, as the astogenetic pattern is a simple but distinctive one, and the ontogenetic changes during colony life are not profound.

Lanceopora d'Orbigny (1852) was introduced for Recent *L. elegans* from Malacca (d'Orbigny, 1852: 187(bis), pl.680, figs 7-10), and is almost certainly a senior synonym of *Parmularia*. D'Orbigny's figures of *L. elegans* depict the budding pattern (including the marginal kenozooidial and extrazoidial structures) and show circular orifices of autozooids surrounded by a distinct raised peristome. The range of orifice shapes is wide among species assigned to *Parmularia* and *Lanceopora*. This range is so wide, the orifice shape might be a useful, subgeneric character. The circular orifices were fully discussed by Harmer (1957), who was undecided as to the synonymy of the two generic names (see Hastings in Harmer, 1957: 983 footnote). The type speci-

men of *L. elegans* no longer exists (Canu & Bassler, 1929: 398). The type colony was minute (less than 4mm long) and sexually immature, without any ovicells. The species will probably never be recognized again with certainty, especially as several different species of *Lanceopora* are known from the Indonesian and Australasian regions. Unlike *L. elegans*, the first Australian *Parmularia* had distinctly sinuate orifices. Until a neotype for *Lanceopora* is chosen, and in view of the frequent use of *Parmularia* in Australian literature, the species discussed here are referred to *Parmularia*.

Specimens were bleached in sodium hypochlorite solution and coated with AuPd for SEM. Abbreviations used: BMNH, Natural History Museum, London; WAM, Western Australian Museum; QM Queensland Museum.

STRUCTURE OF *PARMULARIA* COLONIES

Colonies appear to be bilaminar, the zooid orifices opening on identical faces. There is only a single, central lamina, which is a basal wall common to both zooidial expanses. The lamina is pierced by septulae which allow communication between zooids of either face (Cook & Chimonides, 1985: fig. 4). Usually, at the earlier astogenetic stages, the colony is lanceolate, with several distally budded series. In several species, this is followed by lateral and disto-lateral series, which eventually form a discoid or trilobed colony. Zooids at the margins, especially where further growth has ceased, are usually kenozooids,

formed by basal calcified lamina, and shallow lateral walls, with a cuticular frontal wall. Towards the colony's base (the earlier astogenetic regions), these kenozooids become extrazoidal, as the lateral walls are marginally deficient. They form a narrow band of turgid coelomic tissue, bounded by cuticle and communicating with the extrazoidal rhizoid system. Later in astogeny, this system may produce extensions that form secondary rhizoids (Harmer, 1957).

In life, quite large colonies (4cm in diameter) are supported several centimetres above the bottom sediment by the wide, turgid, extrazoidal rhizoid, which is deeply buried, and divided terminally into numerous rootlets with adhesive cuticle. Calcification of the extrazoidal structures surrounding the origin of the rhizoid becomes much changed during ontogeny. The area becomes thickened by calcification, and is partitioned into a complex of partially opened chambers (Canu & Bassler, 1929; Harmer, 1957). At no time is communication between the zooids and the rhizoids interrupted because damaged rhizoids can be repaired and their turgidity regained (Cook & Chimonides, 1985, fig. 2).

The frontal shield of all autozooids consists of an interior, cryptocystidean calcified wall, overlain by a hypostegal coelom and bounded by frontal cuticle. Frontal septulae, which communicate with the visceral coelom, are placed marginally, especially at the distal and proximal corners of zooid frontals (Cook & Chimonides, 1981, 1985). Other pores are present in the frontal calcification, which may be thickened during ontogeny, particularly round the orifice, which then becomes sunken and obscured. The frontal calcification may be tuberculate, rising into suboral mucros in some species.

Autozooids are monomorphic, becoming larger with astogeny; their orifices may be variously rounded or sinuate proximally, with or without condyles and spinous outgrowths. Brooding zooids are produced fairly late in astogeny, and often have larger, wider orifices than the autozooids, although the kind and degree of dimorphism varies from species to species. Ovicells are prominent; the outer calcification formed from proximally directed outgrowths from the frontal shields of two or more autozooids placed distally to the maternal zooid which produces the egg. Ovicells often show distinct 'suture lines' (Harmer, 1957), which may indicate the number of distal contributory zooids. Ovicells are closed by the brooding zooid operculum, although the position of the operculum varies with preservation

and the developmental state of the ovicells. Several species possess large, interzooidal avicularia, which may have triangular or rounded mandibles, but adventitious avicularia have not been reported.

SYSTEMATICS

Family relationships of *Parmularia* have been discussed by Harmer (1957: 985, 1087, footnote), who discounted an earlier suggestion by Livingstone (1928) that the genus had a close relationship with *Emballothea* Levinsen. Harmer reasoned that the orifices in *Parmularia* were sinuate (unlike those of *Emballothea*) and the colony growth forms were totally dissimilar in the two genera. The orifice shape of all species of *Emballothea* is admittedly non-sinuate, but, as shown below, not all species of *Parmularia* have sinuate orifices. The kinds and degree of dimorphism of brooding zooids, and the structure of the ovicells is the same in both *Emballothea* and *Parmularia* and, in these characters, both genera greatly resemble a third genus, *Calypsothea* Harmer. However, there is a continuity among variable characteristics in all three genera, and Dumont (1981) has discussed the difficulties that have arisen from past attempts to define, or distinguish between, *Emballothea* and *Calypsothea*. *Calypsothea* was introduced by Harmer (1957: 1008) to accommodate species with a sinuate or rounded orifice, which had previously been assigned to *Emballothea*. Surprisingly, he did not discuss the similarities between *Calypsothea* and *Parmularia*, particularly as *Calypsothea* possessed sinuate orifices, the supposed distinction between *Parmularia* and *Emballothea* (see above).

A further similarity between some species of *Calypsothea* and *Parmularia* is the occurrence of large, interzooidal avicularia. These heterozooids have mandibles with robust sclerites and, in some cases, possess lophophores and viscera. Their function is unknown. Interzooidal avicularia occur in *Calypsothea capitifera* (Canu & Bassler, 1929), *C. conica* Cook (1965), *Calypsothea* sp. Harmer (1957), *Parmularia quadlingi* (Haswell, 1880, according to Livingstone, 1926) *P. cylindrica* (Canu & Bassler, 1929, according to Harmer, 1957) and *P. occidenta* sp. nov. Adventitious avicularia occur in most species of *Emballothea* and *Calypsothea* but, as noted, are apparently completely absent in *Parmularia*.

Although the colony form of *Parmularia* differs from that of all species of *Emballothea*,

which is encrusting, it is of interest that several species of *Calypotheca* exhibit equally distinctive, but different, adaptations of growth which are associated with life in a sand-fauna environment. Lunulitiform, rooted colonies occur in *C. orbicularis* Harmer and *C. circularis* Harmer (Harmer, 1957) and lunulitiform, unrooted colonies in *C. conica* Cook (1965).

A similar diversity of colony form, which also includes different kinds of adaptation to a sand-fauna existence, occurs in the Microporellidae (*Microporella*, *Flustramorpha* and *Diporula*; Cook, 1968; Hayward & Cook, 1983), Celleporariidae (*Celleporaria* and *Sphaeropora*; Harmer, 1957; Cook & Chimonides, 1981), Eurystomellidae (*Eurystomella* and *Selenariopsis*; Cook & Chimonides, 1981), and Petraliellidae (*Mucropetraliella* and *Riscodopa*; Cook & Chimonides, 1981; Gordon, 1989). In all respects other than colony form, the three genera *Emballothea*, *Calypotheca* and *Parmularia* comprise a fairly natural grouping that differs from other groups of genera often included informally in the family Schizoporellidae in the structure of the ovicells and the frequency of dimorphism of the brooding zooids.

Class GYMNOAEMATA Allman, 1856

Order CHEILOSTOMIDA Busk, 1852

Family PARMULARIIDAE Canu & Bassler, 1927

Parmulariidae Canu & Bassler, 1927: 21, 35.

Lanceoporidae Harmer, 1957: 983.

Type genus. *Parmularia* MacGillivray.

Genera included. *Parmularia* MacGillivray, 1887. *Lanceopora* d'Orbigny, 1852, *Emballothea* Levison, 1909 and *Calypotheca* Harmer, 1957.

DESCRIPTION

Cryptocystidean Ascophora with primary orifice rounded distally, but variable proximally; spines absent. Brooding zooid orifices usually dimorphic, large and wide. Ovicells usually formed by proximal extensions of calcified frontal shields of more than one distal zooid. Adventitious and interzooidal avicularia present or absent.

REMARKS

Canu & Bassler (1927) introduced Parmulariidae, in spite of their use of 'Parmulariidae Maplestone 1912' as a reference, both in 1927 and in 1929 (p.397). This misquotation of the

authorship was followed by Wass & Yoo (1983: 340) but it should be noted that Harmer (1957: 983) ascribed the family name to Canu & Bassler. Maplestone used *Parmularia* in 1910 and 1913: a work dated 1912 does not seem to exist.

Parmularia MacGillivray, 1887

Parmularia MacGillivray 1887: 191, 211.

Lanceopora d'Orbigny' Harmer, 1957.

Type species. *Eschata obliqua* MacGillivray, 1869.

DESCRIPTION

Colonies erect, compressed, leaf-like, with orifices opening on both faces, supported by one or more turgid, extrazooidal cuticular rhizoids. Autozooids with orifices straight, rounded or sinuate proximally. Brooding zooids with larger, often distinctly dimorphic orifices. Adventitious avicularia absent; interzooidal avicularia sometimes present.

REMARKS

Harmer (1957) gave a key to Indo-west Pacific species and introduced *Lanceopora formosa* (Harmer, 1957:987, pl.66, figs 10-13, 103-105), an elongated, lanceolate, very delicate species from the East Indies. He also redescribed *L. cylindrica* Canu & Bassler (1929) from the Philippines and somewhat doubtfully assigned his own Siboga material, which had interzooidal avicularia, to this species.

Schizoporella flabellata Maplestone (1902: 68, pl. 7, fig. 10), from the Tertiary of Victoria, was later included in *Parmularia* by Maplestone (1910, 1913). Ovicells do not seem to have been described in fossil specimens, which are usually fragmented or very small and sexually immature. The degree of dimorphism of the Tertiary species is therefore unknown, but the small, distinct, rounded sinus of the autozooid orifice has usually been taken as an indication of a close relationship between *P. flabellata* and *P. obliqua*, the Recent type species of *Parmularia* (see Livingstone, 1924:190). Stach (1935) referred his Lower Pliocene Australian specimens to *P. obliqua*.

Parmularia obliqua (MacGillivray) (Fig. 1a)

Eschata obliqua MacGillivray, 1869: 137. 1880: 39, pl. 48, figs 1, 1a, 1 b.

Parmularia obliqua MacGillivray, 1887: 211. Maplestone, 1910: 42, pl. 10. 1913: 360, pl. 28, fig.

11. Livingstone, 1924; 190, pl. 23, figs 1,2, pls 25,26, figs 1a-c. Stach, 1935: 343, pl. 12, fig. 5. Wass & Yoo, 1983: 340, figs 60-61. Cook & Chimonides, 1985: 72, fig. 1.

Schizoporella flabellata Maplestone, 1902: 68, pl. 7, figs 10, 10a.

Lanceopora obliqua Harmer, 1957: 990, fig. 102. cum.syn. Bock 1982: 383, figs 9, 28a,b, pl.28.6.

MATERIAL EXAMINED

BMNH: 1884.11.4.14, Port Phillip; 1899.5.1.1080, Curtis Is., Bass Strait; 1899.7.1.43 & 84, Port Phillip, Victoria; 1912.5.1.3A, South Australia; 1965.2.2.1, Holothuria Bank, northwestern Australia, 44-62m (with *P. occidenta* q.v.); 1975.7.28.29, off Adelaide, 36-64m; 1987.1.10.2, off Jurien Bay, Western Australia, 137m. WAM: off Jurien Bay, Western Australia 137m.

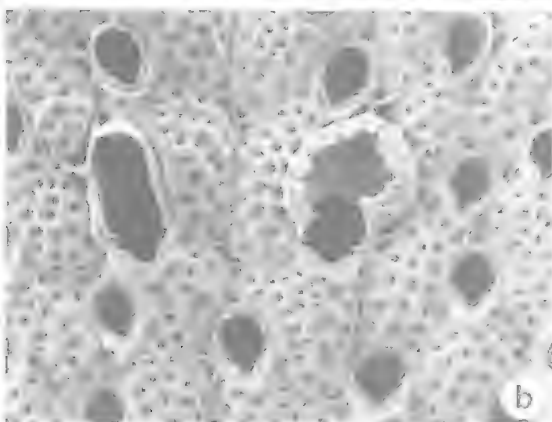
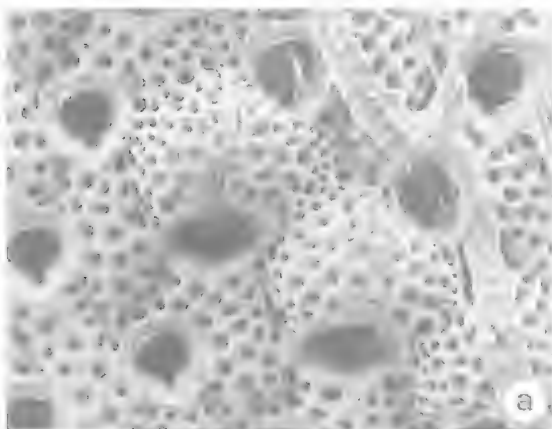


FIG. 1. a, *Parmularia obliqua*, Jurien Bay, autozooids and brooding zooids, $\times 57$. b, *P. quadlingi*, Townsville, autozooids and one broken ovicell of brooding zooid, with one vicarious avicularium, $\times 49$.

DESCRIPTION

Colonies kidney-shaped or nearly circular; wide, up to 4cm in diameter. Little evidence of an early lanceolate form. Autozooid orifices with very small, triangular-to-rounded proximal sinus and large, paired condyles. Brooding zooid orifices often large, wide and slit-like, sometimes with paired distal, but proximally directed, processes. Ovicells often very large, produced late in astogeny, with suture lines. Interzooidal avicularia absent.

REMARKS

P. obliqua has been reported from the coasts of Victoria, South Australia and Western Australia. With such a large distribution, some variation in characters may be expected. This seems to be most expressed in the degree of dimorphism of the brooding zooids. Specimens illustrated by Bock (1982) and Wass & Yoo (1983) show very wide, almost slit-like orifices of brooding zooids. The colonies from Jurien Bay have more open, proximally curved brooding zooid orifices, but a similar small autozooid sinus (Fig. 1a). Some specimens show a wide range of variation within a single colony.

Parmularia quadlingi (Haswell) (Fig. 1b)

Lepralia (*Schizoporella*) *quadlingi* Haswell, 1880: 39, pl. 2, fig. 2.

Parmularia quadlingi Livingstone, 1926: 85, pl. 5, fig. 6, pl. 6, figs 1-2.

Lanceopora quadlingi Harmer, 1957: 990, pl. 66, fig. 11 c, 18, fig. 106.

MATERIAL EXAMINED

BMNH: 1910.6.16.5 (labelled 'Co-type'), Holborn Is., Queensland; 1935.2.22.1, Torres Strait; 1975.7.28.27, Torres Strait (figured by Harmer, 1957); 1975.7.28.28 (labelled 'from collection described by Haswell'), Port Denison, Queensland; 1987.1.10.1, off Townsville, Queensland, 1981, P. Arnold.

DESCRIPTION

Colonies lanceolate at first, becoming trilobed, up to 2cm in diameter. Autozooids with a small rounded or subtriangular sinus. Brooding zooid orifices larger. Interzooidal avicularia with an elongated, subtriangular mandible present.

REMARKS

Livingstone (1926) redescribed *P. quadlingi* from Haswell's 'type' (specimen in the Austra-

lian Museum, Sydney) and from his own material which was also from Queensland (and which possessed rhizoids). He noted that the 'type' specimen was fragmentary, and that it did not include any large, interzooidal avicularia. The autozooid orifices, each with a small, rounded,

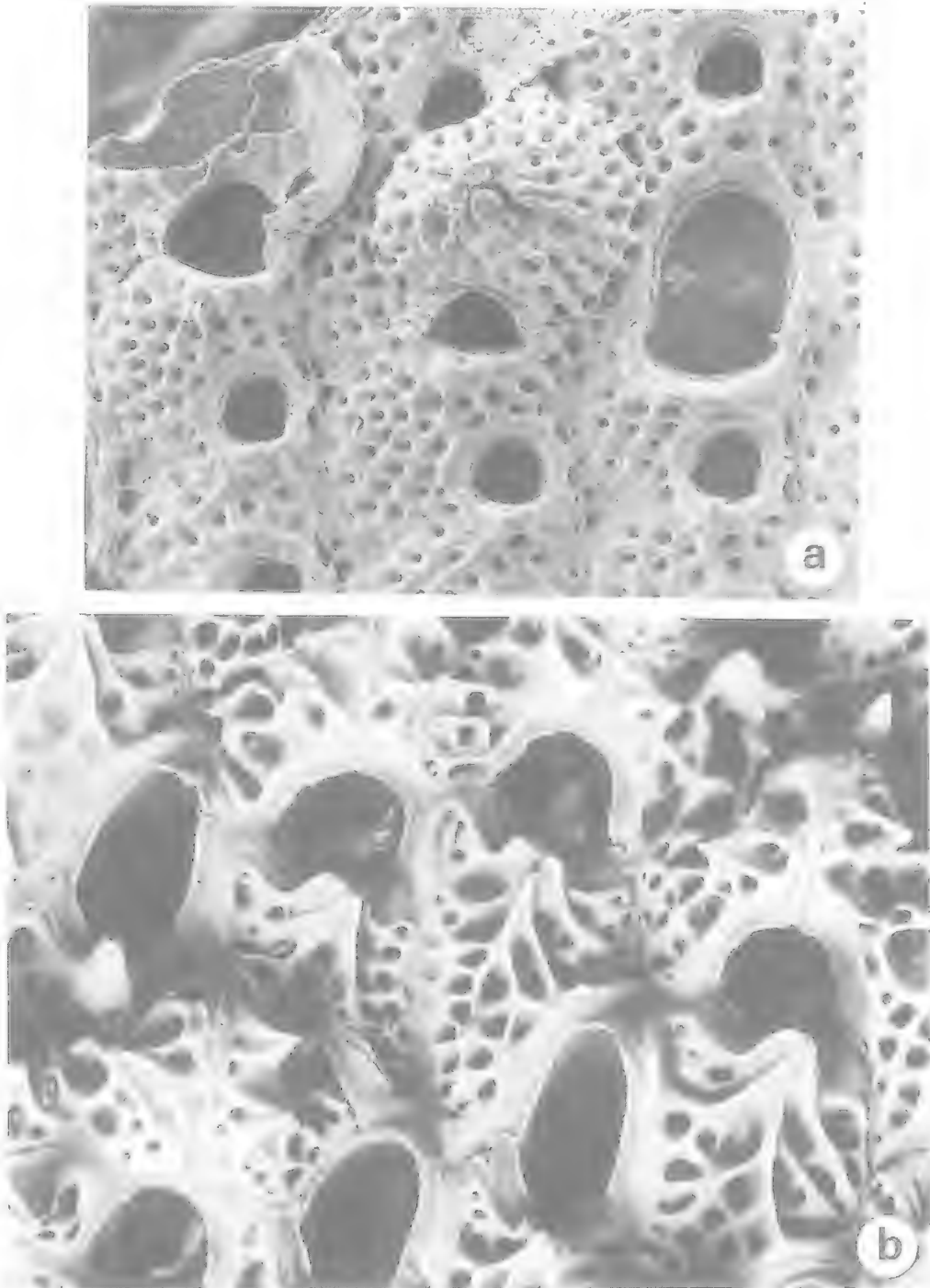


FIG. 2. a, *Parmularia occidenta*, Holothuria bank, autozooids, one brooding zooid and one vicarious avicularium, $\times 73$. b, *Parmularia arnoldi*, Townsville, autozooids and brooding zooids with ovicells, $\times 85$.

proximal sinus, illustrated by Livingstone (1926) are similar to those figured by Haswell (1880). Furthermore, both illustrations show similar ovicells and relatively little dimorphism of the brooding zooid orifices.

The BMNH 'Co-type' (1910.6.16.5) is a minute fragment comprising 8 zooids and 4 brooding zooids. It differs from Livingstone's figure in having larger autozooid orifices with subtriangular sinus and distinct condyles. No interzooidal avicularia are present. There is, however, some dimorphism of brooding zooid orifices. Harmer's figure (1957: pl. 66, fig. 18) shows autozooids with orifices resembling those figured by Haswell and Livingstone. However, the one brooding zooid orifice shown has a wide proximal curved edge with no sinus. Material from the same collection (Haddon) and locality (Torres Strait) in the BMNH (1935.2.22.1), which was also examined by Harmer, shows that the shape of the autozooid orifice may change with astogeny. The autozooids nearer the growing edge may have orifices with a wide subtriangular sinus. The brooding zooid orifices are larger and have a wider sinus which can be obscured by raised proximal calcification. The interzooidal avicularia resemble Livingstone's figure.

The specimen from Townsville (BMNH 1987.1.10.1, Fig. 1b) also has autozooid orifices with a subtriangular sinus, and a dimorphism of the brooding zooids is evident. The mandible of the interzooidal avicularia are proportionally much longer than those illustrated by Livingstone (1926: pl. 6, fig. 1) and by Harmer (1957: pl. 66, fig. 18). With this wide range of variability, *P. quadlingi* sensu lato may include the Siboga specimens from the Sulu Archipelago, which Harmer (1957) assigned to *P. cylindrica*. *P. cylindrica* Canu & Bassler (1929) was not described with interzooidal avicularia and none are present in the material examined (*P. cylindrica*, Bassler Collection BMNH 1931.12.30.153, Philippines). The interzooidal avicularia figured by Harmer seem to have had very short triangular mandibles and, like those of *P. quadlingi*, are narrower than those of *P. occidenta*.

P. quadlingi may prove to be a complex of more than one form or a single variable species. It appears to be confined to the coast of Queensland and the Torres and Makassar Straits.

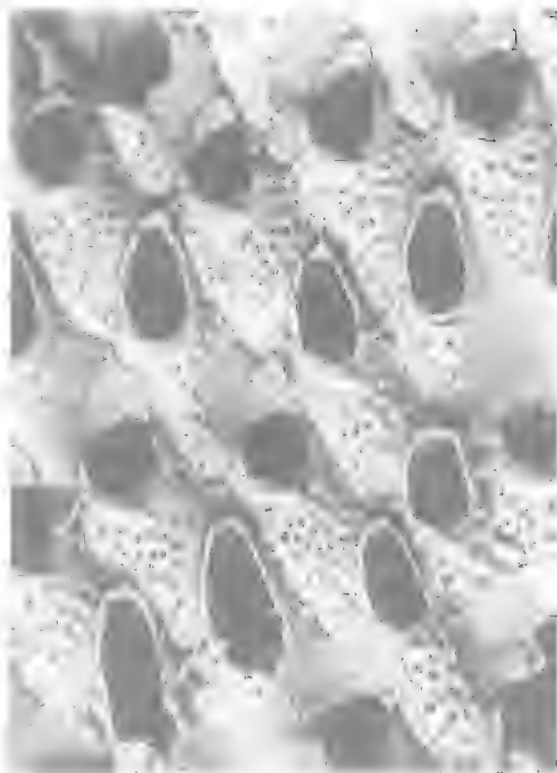


FIG. 3. *Parmularia arnoldi*, Townsville, autozooids and maternal brooding zooids with incipient ovicell development, $\times 48$.

***Parmularia occidenta* sp. nov.**
(Fig. 2a)

MATERIAL EXAMINED

HOLOTYPE: BMNH 1892.1.28.40A, Holothuria Bank, northwestern Australia, 27m.

PARATYPES: BMNH: 1892.1.28.40B, as for holotype; 1987.1.10.3, Holothuria Bank, 44-62m, (with *P. obliqua*).

ETYMOLOGY

Latin *occidentis*, west.

DESCRIPTION

Colonies lanceolate in early astogeny, becoming discoid or reniform, up to 2cm wide, with laterally directed zooidal series and zones of ovicells. Autozooid orifices somewhat elongated, curved, but not sinuate proximally, with small, spine-like, paired condyles near the proximal margin. Brooding zooid orifices wide, slightly curved proximally. During ontogenetic thickening a mucronate process develops proximally to the orifice and a similar mucro may appear on the

frontal surface of the ovicell. Interzoooidal avicularia very large and wide, but with a short, narrow frontal shield that forms a raised shelf proximal to the mandible. Mandibles large, wide, rounded distally, with robust paired sclerites.

REMARKS

The holotype colony is dry but has a well developed extrazoooidal calcification indicating that the rhizoid would have been 7mm wide at its origin. The accompanying paratype colony is only 1cm wide but has a rhizoid >1cm long and 2mm wide at its origin. The interzoooidal avicularia often develop mandibles late in ontogeny and may be seen in a partially developed condition at some distance from the growing edge. *P. occidenta* resembles *P. mcneilli* Livingstone (1924: 194, pl. 24, figs 1,2, pl. 25, fig. 2), but differs by very large interzoooidal avicularia. *P. occidenta* is known only from NW Australia.

Parmularia arnoldi sp.nov. (Figs 2b, 3)

Parmularia sp. Cook & Chimonides, 1985:71, figs 2, 3A,B.

MATERIAL EXAMINED

HOLOTYPE: QM G21260, off Townsville, Queensland, 10-15m, large specimen 28mm in length with rootlet. PARATYPES: QM: G21261, as for holotype colony fragments; G21259, Cleveland Bay, Queensland (19°13'S, 146°58'E), 23 August 1986, P.Arnold & A. Birtles, two colony fragment. BMNH: 1986.7.30.1, off Townsville, Queensland, 10-15m, numerous colony fragments, some with rootlets.

ETYMOLOGY

For Peter Arnold, Museum of Tropical Queensland.

DESCRIPTION

Early astogenetic stages lanceolate. Colonies becoming large, >4cm in diameter, discoid or reniform. Autozoooid orifices very elongated, narrowing distally, deeply curved proximally, but without a distinct sinus; lateral condyles small. Distal rim of orifice raised, often with thin, crenulated processes overhanging the operculum. During ontogeny, a long mucronate process is developed proximally that obscures the secondary orifice. Brooding zoooid orifices not elongated, slightly wider and proximally sinuate. Ovicells very large, with two or three suture lines, becoming tuberculate with large processes on the frontal surface. Avicularia absent.

REMARKS

The autozoooid orifices distinguish this species from all others. The similarity between the autozoooids of *P. arnoldi* and the avicularian zoooids of *P. quadlingi* is striking (cf. Figs 1b, 2b). The raised distal process in *P. arnoldi* often overhangs the orifice and is reminiscent of the similar processes which occur in the dimorphic zoooids of *Uscia mexicana* Banta (1969; see also Cook, 1979). The minute peg-like condyles are present in both autozoooids and brooding zoooids of *P. arnoldi*. Apart from not being as elongated, the brooding zoooid orifices are not very dimorphic, being only slightly wider and having a shallow proximal sinus. Autozoooids and brooding zoooids frequently occur in sloping or horizontal series of alternating astogenetic generations (Fig. 2b). Each ovicell originates as a minute lamina growing distally from the maternal zoooid orifice; this becomes the inner entoocelial capsule. Simultaneous changes to the distal zoooid or zoooids include the obscuring of frontal pseudopores by secondary calcification and the gradual delineation of a circular distal depression (Fig. 3). This area marks the extent of the future ovicell and, later in ontogeny, the edges of the area (which is a frontal extension of the cryptocystal frontal shield of the distal zoooids) become increasingly raised and eventually curve over and fuse medially, forming the ectooecium and enclosing the entoocelial capsule contributed by the proximal maternal brooding zoooid. Suture lines occur where more than one distal zoooid has contributed to the ectooecial cover, and the ovicells become sunken as secondary calcification thickens the entire colony frontal. Large, irregular pores in the calcification are 'carried up' from the areolae above the marginal frontal septulae and these, together with the raised mucronate processes, give the colony an appearance unlike that of any other species (Fig. 2b).

Many colonies were collected alive from off Townsville in 1982. These possessed extensive, turgid rhizoid systems. Most of each rhizoid was buried in the muddy sand of the sea bottom, but supported the bilaminar 'head' of feeding zoooids several centimetres above the surface of the substratum. The larval behaviour, the settlement and early astogeny of *P. arnoldi* have been described (as *Parmularia* sp.) by Cook & Chimonides (1985).

A small, worn fragment with zoooids with similar, elongated orifices (BMNH 1982.2.23.498, Arafura Sea, off the Northern Territory, Australia, 68-72m) may belong to *P. arnoldi*. If con-

firmed by further specimens, this would extend its range across the northern coast of Australia.

ACKNOWLEDGEMENTS

We thank Dr P. Arnold (Museum of Tropical Queensland) and Dr A. Birtles (James Cook University of Northern Queensland) for their help in collecting and maintaining living colonies of *Parmularia*, and Dr J.D.D. Bishop (Port Erin Marine Laboratory, UK) for constructive criticism.

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TWO BIVALVES FROM THE MIDDLE DEVONIAN BURDEKIN FORMATION, NORTH QUEENSLAND

ALEX G. COOK

Cook, A.G. 1993 06 30: Two bivalves from the Middle Devonian Burdekin Formation, north Queensland. *Memoirs of the Queensland Museum* 33(1): 49-53. Brisbane. ISSN 0079-8835.

The bivalves *Phenacocyclus pohli* LaRocque and *Modiomorpha mitchellae* sp.nov. are found within the Burdekin Formation, to the north of Charters Towers, north Queensland. They represent respectively the first lucinid and modiomorph described from these strata. *M. mitchellae* sp.nov. is characterised by its large size and elongate shape. □ *Mollusca, Bivalvia, Lucinidae, fossil, Phenacocyclus, Modiomorpha mitchellae, new species, Queensland, Middle Devonian, Burdekin Formation.*

Alex G. Cook, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 14 August, 1992.

Collections of molluscs from the Middle Devonian (Givetian) Burdekin Formation have yielded two bivalve genera previously unreported from this formation, *Phenacocyclus pohli* LaRocque and *Modiomorpha mitchellae* sp.nov.

Stratigraphic nomenclature for the area is outlined in Wyatt & Jell (1980) and Lang et al. (1990). The Fanning River Group is divided into three formations—the Big Bend Arkose, mostly coarse grained siliciclastics is overlain by the Burdekin Formation, a dominantly limestone sequence, which in turn is overlain by the Cultivation Gully Formation, a predominantly siliciclastic unit. In the Burdekin Downs area (Fig. 1), the location of *Phenacocyclus pohli* LaRocque, the Burdekin Formation is about 90m thick and the Cultivation Gully Formation has been eroded. In the Paynes Lagoon area (Fig. 1), the locality of *Modiomorpha mitchellae* sp.nov., the only manifestation of the Burdekin Formation is a 2 to 5m thick molluscan shell bed that rests unconformably on Precambrian Basement.

In previous investigations of the molluscan fauna, Etheridge (1917) described a single gastropod from the Group and Heidecker (1959) described three gastropods and the two bivalve taxa from the Big Bend area: *Tanaodon louderbacki* Kirk and *Neoactinodonta amygdalina* Heidecker. Both Heidecker's species have been reassigned to *Tanaodon louderbacki* Kirk by Pojeta, Zhang & Yang (1986). Zhen (1990) reviewed the gastropod biofacies found at the base of the Fanning River Group, but did no further taxonomic investigations of the molluscan fauna. Cook (in press) describes a fourth genus of gastropod from the Big Bend Arkose and lower Burdekin Formation.

The Burdekin Formation has been assigned a late Eifelian to Givetian age based on limited conodont data, rugose coral associations, and the

presence, in abundance, of *Stringocephalus* sp. No precise zonal ages for the localities given in this work are available but the coral fauna associated with both molluscs suggests a Givetian age (Zhen, 1990).

SYSTEMATIC PALAEOLOGY

Phylum MOLLUSCA

Class BIVALVIA Linné, 1758

Subclass HETERODONTA Neumayr, 1884

Order VENEROIDEA Adams and Adams, 1856

Superfamily LUCINICOIDEA Fleming, 1828

Family LUCINIDAE Fleming, 1828

Phenacocyclus LaRocque, 1950

TYPE SPECIES

Phenacocyclus pohli LaRocque by original designation from the Middle Devonian of Michigan.

DIAGNOSIS

Equivalved, irregularly rhomboidal lucinoideans with a prominent posterodorsal radial sulcus, slight anteroventral embayment and comarginal ornament. Hinge is straight and short with small umbones, narrow escutcheon and small lunule. Internal molds with posteroventral notch, two large elongate adductor scars and prominent irregular sigmoidal grooves. Posterior adductor deeper and narrower than anterior scar. Dentition small and poorly known: one probable small lateral tooth and probable small cardinal tooth.

REMARKS

Phenacocyclus, according to LaRocque (1950) is separated from *Paracyclus* Hall by the posterodorsal sulcus, the arrangement of the adductors, the presence of a strong posteroventral notch and

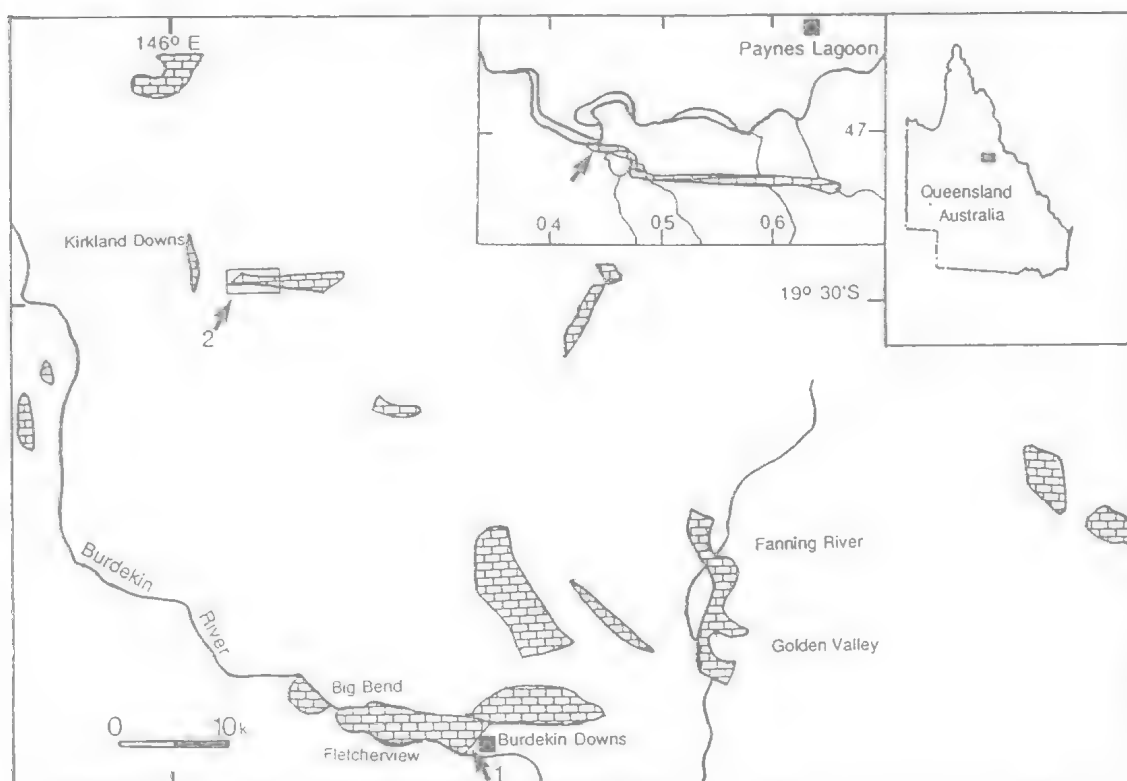


FIG. 1. Outcrop pattern for the Fanning River group within the Townsville Hinterland, showing collection localities (arrows) for *Phenacocylas pohli* LaRocque (1) and *Modiomorpha mitchellae* sp.nov. (2).

the sigmoidal grooves on internal molds. It differs from *Crassatellopsis* Beushausen and *Montanaria* Spriestersbach on the basis of size of the dentition. The genus has been placed in the Lucinidae by Chavan (1969).

***Phenacocylas pohli* LaRocque** (Fig. 2)

MATERIAL EXAMINED

Nine conjoined specimens with shell intact and mostly free from host lithology of impure carbonate wackestone. Only 6 of the specimens are sufficiently complete to provide size data (Table 1). Material housed in Queensland Museum: QMF 22528, QMF 22529; James Cook University JCUF 11806-11812.

AGE AND OCCURRENCE

Present Study: Middle Devonian (Givetian) Burdekin Formation, Fanning River Group. Collected from hill directly behind Burdekin Downs Homestead, NW of Charters Towers, north Queensland. Grid Reference Dotswood: DU 199 011. Middle Devonian Dundee Limestone and Rodgers City Limestone, Michigan, U.S.A.

DESCRIPTION

Medium to large equivalved rhomboidal shells ranging in height from 35-55mm, in length 42-56mm and width 19-25mm. Strong posterodorsal sulcus present. Slight embayment on the anteroventral margin. Thin shelled, with well developed comarginal ornament consisting of fine growth lines overprinted by coarser irregularly spaced rugations. Hinge and internal structures not seen.

REMARKS

Burdekin material is only slightly larger than the type material illustrated by LaRocque (1950)

TABLE 1. Morphometric data for specimens of *Phenacocylas pohli* from the Burdekin Formation. Measurements in mm.

SPECIMEN	HEIGHT	LENGTH	WIDTH
QMF 22528	43	46	24
QMF 22529	39	44	19
JCUF 11806	55	57	25
JCUF 11807	54	56	24
JCUF 11808	46	42	19
JCUF 11810	45	44	19



FIG. 2. a-c. *Phenacocyclus pohli* LaRocque JCUF 11806: a, right valve $\times 0.9$; b, left valve $\times 0.9$; c, dorsal view $\times 1$.

and shows all of the external features described for *Phenacocyclus pohli*. Unfortunately the illustrated adult specimens are restricted to internal molds but juvenile material (LaRocque, 1950 pl. 15, figs 1-7) shows features found also in the Burdekin specimens.

Both LaRocque (1950) and Bailey (1983) suggested that *Paracyclas antiqua* (Goldfuss) may belong to *Phenacocyclus*. In particular *Paracyclas antiqua* (Goldfuss) of Beushausen (1895) shows many of the features of *Phenacocyclus*. The size of Beushausen's (1895) specimens, as given by Bailey (1983) is similar to that of *Phenacocyclus pohli* LaRocque. It is possible that the two are synonymous but determination of this awaits detailed examination of type material of *Paracyclas antiqua* (Goldfuss).

Subclass PALAEOHETERODONTA

Newell, 1965

Order MODIOMORPHOIDA Newell, 1969

Superfamily MODIOMORPHACEA

Miller, 1877

Family MODIOMORPHIDAE Miller, 1877

Modiomorpha Hall & Whitfield, 1869

TYPE SPECIES

Modiomorpha concentrica (Conrad, 1838)

DIAGNOSIS

Modioliform modiomorphids with large wedge-shaped cardinal tooth in left valve, socket

in right valve, weak laterals, rugose growth increments.

Modiomorpha mitchellae sp. nov.

(Fig. 3)

MATERIAL EXAMINED

HOLOTYPE: JCUF 11823; internal mold.

PARATYPES: QMF 22684-85: well preserved internal molds, JCUF 11824-28, QMF 22686, 22687.

OCCURRENCE

Middle Devonian (Givetian), north Queensland Australia. Burdekin Formation, Paynes Lagoon Station, 80km W of Townsville.

DIAGNOSIS

Very large, elongate *Modiomorpha* with medium to coarse comarginal ornament.

DESCRIPTION

Large posteriorly elongate shells, modioliform in outline, up to 150mm long. Shell thick, especially anterodorsally, thinning posteroventrally. A break in shell slope, which runs from anterodorsal margin to posteroventral margin on the internal mold, is a weak ridge. Medium to coarse comarginal ornament preserved on JCUF 11824. Invagination along the hinge indicates large cardinal tooth and socket. Hinge plates relatively thick. Anterior adductor scar is small, subcircular. Quick and catch portions are easily discernible. Dorsally adjacent retractor scar is much smaller, subcircular. Posterior scar not preserved.

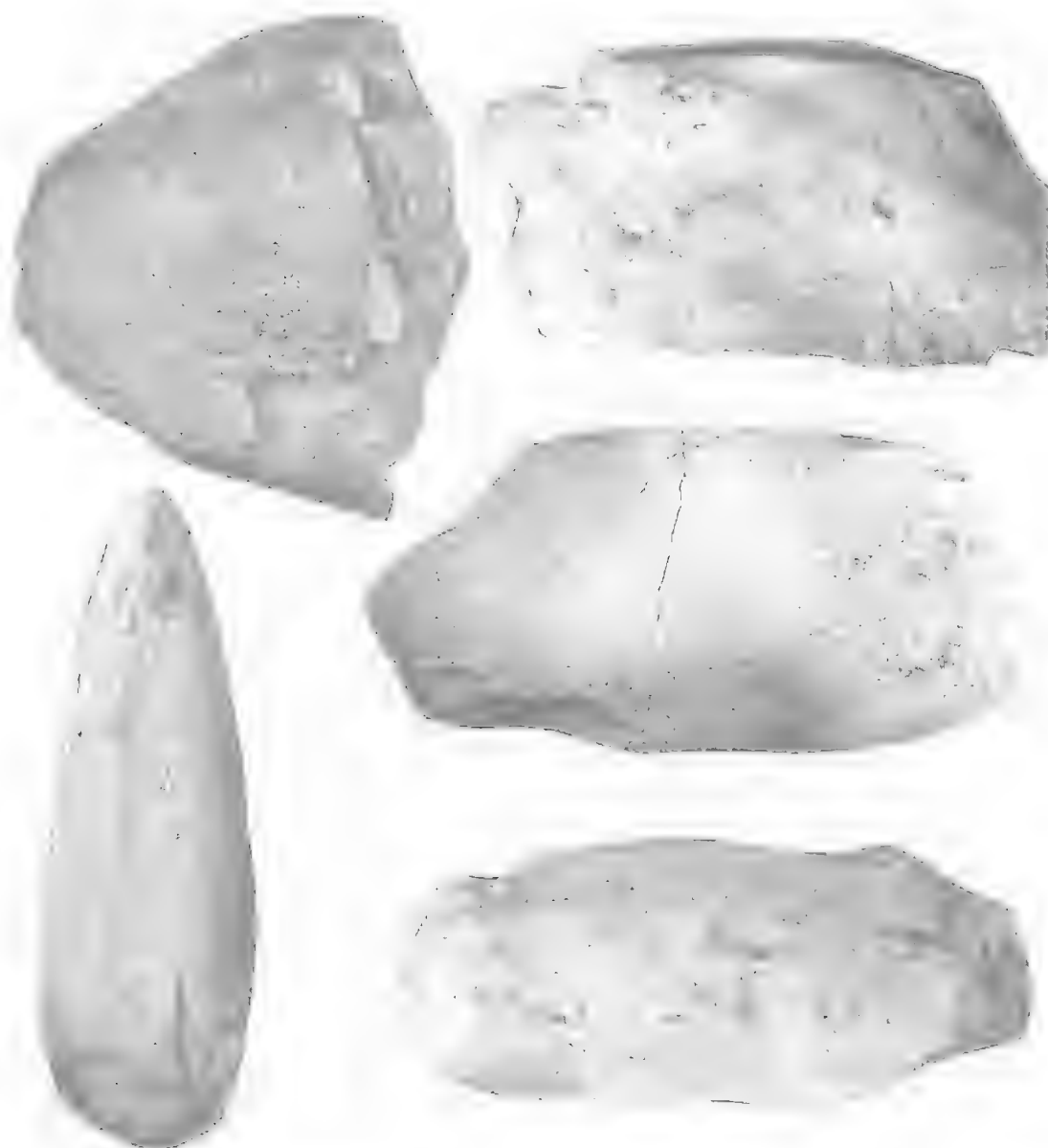


FIG. 3. a-c *Modiomorpha mitchellae* sp. nov: a, Paratype JCUF 11824, external of partial right valve, showing concentric ornament $\times 1.1$; b, Holotype JCUF 11823, internal mold left valve $\times 1$; c, Holotype JCUF 11823, internal mold right valve $\times 1$; d, Paratype QMF 22684, dorsal view of articulated internal mold, showing invagination indicating large cardinal tooth $\times 1$; e, Paratype QMF 22684, internal mold left valve, showing prominent anterior adductor $\times 1$.

REMARKS

The characteristic musculature, dentition, shape and size ally the material to the genus *Modiomorpha*. It is distinguished by its size and rather elongate shape from other species of *Modiomorpha*. *M. concentrica* (Conrad) described by Bailey (1983), Pojeta, Zhang & Yang

(1986) and *M. oblonga* Zhang 1977 are smaller despite Pojeta, Zhang & Yang's (1986) comment that *M. oblonga* is of large size. *M. herculi* Bradshaw 1991 (in Bradshaw & McCartin, 1991) is substantially smaller. *M. mytiloides* (Conrad, 1841; in Bailey, 1983) is also a small form. There is some disagreement concerning the systematic

position of *Modiomorpha* Hall & Whitfield. Newell's (1965) scheme is followed here, but Pojeta, Zhang & Yang (1986) express a different view.

ETYMOLOGY

Named for R. L. Mitchell for her contributions to the study of modern mollusca from the Townsville area.

ACKNOWLEDGEMENTS

R. A. Henderson is thanked for endless help and provision of specimens collected by D. H. Wyatt from Paynes Lagoon. JCU Merit grants in 1990 and 1992 contributed to this work, as did the Queensland Museum by the provision of services. M. Wade and P. A. Jell are thanked for their encouragement. The owners of Paynes Lagoon and Burdekin Downs are thanked for their hospitality.

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A RECORD OF THE COMMON PLANIGALE AT MYORA SPRINGS: THE FIRST DASYURID FROM NORTH STRADBROKE ISLAND. *Memoirs of the Queensland Museum* 33(1): 54. 1993. - A Common Planigale (*Planigale maculata*) was captured at Myora Springs (153°25'E, 27°29'S), North Stradbroke Island on February 11, 1993. The animal was trapped during a survey by Griffith University staff and third-year students, conducted as part of a 'field ecology' course. The trapping effort at Myora Springs consisted of four pitfall traps (20 litre buckets c.38cm deep and 30cm diameter), each situated half-way along a 20m drift fence, as well as 40 small Elliott traps, all of which were set over four nights during February 9-12, 1993. The planigale was caught in one of the pitfall traps.

The Myora Springs region lies on the western edge of North Stradbroke Island, where Capembah Creek drains into the ocean. In this area there is a complex mixture of plant communities, including rainforest, *Melaleuca quinquenervia* forest and woodland, sedgeland, eucalypt forest and woodland, and disturbed areas. The habitat in which the traps were set was mapped by Coutts (1992) as partly disturbed closed forest, incorporating patches of simple notophyll vine forest dominated in part by *Melicope elleryana* with *Eucalyptus robusta* emergents and in part by *Callitris columellaris* with *Eucalyptus* spp. emergents; grading on its southern side into an open forest dominated by *Melaleuca quinquenervia* with *Eucalyptus robusta* emergents, and on the eastern side into open forest dominated by *E. pilularis*. The area of closed forest is not much more than one hectare, but is the only area of notophyll vine forest on North Stradbroke Island (Kikkawa, 1975).

The trapped specimen was a young male (testes clearly visible although not very large), of weight 6.0g, head and body length 59mm and tail length 48mm. After being caught it was retained in captivity for three days, during which period it was taken to the Queensland Museum where its identity was confirmed (S. Van Dyck) and it was photographed. It was then released on Stradbroke Island at the point of capture.

This specimen is significant because it is the first record of the family Dasyuridae from North Stradbroke Island. Three dasyurids (*Antechinus flavipes*, *Sminthopsis murina* and *Planigale maculata*) have been recorded from Fraser Island (Van Dyck, 1991), but none from either North Stradbroke or Moreton Islands, in spite of extensive survey effort on North Stradbroke Island (Martin, 1975; Barry & Campbell, 1977; Van Dyck, 1991). *Planigale maculata* was, however, recorded some time ago (1960) from nearby Russell Island (Van Dyck, 1983).

The present new record may be a consequence of using pitfall traps for sampling. Trapping with baited Elliott traps during the past ten years at Myora Springs during annual Griffith University field excursions (typically with 50-100 traps set over three nights each year) has usually yielded high capture rates of *Melomys* species (*M. burtoni* or *M. cervinipes*), moderate capture rates of *Rattus lutreolus*, and occasional captures of *Isodon macrourus*. In 1993, *Mus musculus* was also captured in the area for the first time, probably a

consequence of recent residential development nearby. Pitfall traps were set for the first time in 1993, and four pitfalls set over four nights caught one *Planigale maculata* and two juvenile *Melomys* sp.

The absence or relative scarcity of dasyurid marsupials on the large sand islands of Moreton Bay is a puzzling biogeographical pattern (see Barry & Campbell, 1977). The lack of dasyurids from these islands cannot be simply a consequence of lack of appropriate sampling, since *Antechinus* spp., if present, should have been caught using conventional baited traps. The distribution of habitat may also be a contributing factor: Stradbroke and Moreton Islands are dominated by 'dry' sclerophyll and heathland communities on soils very low in nutrients (see for example Clifford & Specht, 1979), whereas Fraser Island supports large areas of the moister forest types. Frequent fires on North Stradbroke Island have probably also influenced the habitat available to dasyurids (Martin, 1975). Further pitfall sampling in other parts of North Stradbroke Island would be required to determine whether *P. maculata* occurs throughout the island, or is localised within particular areas such as Myora Springs.

Acknowledgements

Thanks to Steve Van Dyck (Queensland Museum) for suggestions and encouragement and to all the staff and students of the 1993 Griffith University 'Field Ecology' course, in particular Nick Cilemo, Jane Hughes and Stuart Bunn.

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G.P. Catterall, Faculty of Environmental Sciences, Griffith University, Nathan, Queensland 4111, Australia: 26 February, 1993.

CHERAX CARTALACCOOLAH, A NEW SPECIES OF FRESHWATER CRAYFISH
(DECAPODA: PARASTACIDAE) FROM NORTHEAST AUSTRALIA

JOHN W. SHORT

Short J.W. 1993 06 30: *Cherax cartalacoolah*, a new species of freshwater crayfish (Decapoda: Parastacidae) from northeast Australia. *Memoirs of the Queensland Museum* 33(1): 55-59. Brisbane. ISSN 0079-8835.

A new species of freshwater crayfish, *Cherax cartalacoolah*, from eastern Cape York Peninsula, Queensland is described and illustrated. The new species most closely resembles *C. robustus* Riek, 1951, which occurs in similar, sand dune habitats in southeast Queensland, and can be distinguished by the morphology of the carapace and first chelipeds. □ Crustacea, Parastacidae. *Cherax*, new species, northeastern Australia, Cape York Peninsula, freshwater, taxonomy, biology.

John W. Short, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 3 March, 1993.

Australian species of *Cherax* Erichson were last revised by Riek (1969), who listed 27 species. Short (1991) described *C. nuciifraga* from the Northern Territory.

Cherax cartalacoolah sp.nov. was brought to my attention in October 1991 by Mr Rolly McKay, Queensland Museum. Only two immature specimens and a number of carapace fragments and chelae were available but this was sufficient to establish that the species was new to science. A Queensland Museum expedition to the Cape Flattery area in November 1992 by Mr Peter Davie and myself, collected further material including mature adult specimens.

Abbreviations used in text: QM, Queensland Museum; CL, postorbital carapace length; T, thoracic sternite, T6, thoracic sternite six etc.

***Cherax cartalacoolah* sp.nov.**
(Figs 1-3, 4A,B)

MATERIAL EXAMINED

HOLOTYPE: QM W18224, ♂ (30.3mm CL), Cape Flattery, second creek south of headland, 14°59.2'S, 145°20.2'E, supralittoral, in burrow amongst rushes fringing lagoon, peaty sand, freshwater, pH 5, hardness 40ppm, water temperature 33°C, dissolved oxygen 1.7ppm, altitude c.10m, 16/11/1992, J. Short, P. Davie. **ALLOTYPE:** QM W18225, ♀ (23.6mm CL, right cheliped missing, left damaged at base of pollex), from same burrow as holotype.

PARATYPES: QM W17231, ♀ (14.4mm CL), Arnie's Lake, Cape Flattery, 14°58'S, 145°19.5'E, 11/10/1991, R. McKay. QM W17234, ♂ (18.4mm CL), Windmill Lake, Cape Flattery, 14°58'S, 145°17.5'E, 13/09/1991, R. McKay. QM W18223, ♀ (16.2mm CL), Vince's Lake, Cape Flattery, 14°59'S,

145°16'E, supralittoral, burrow in bank of artificial drainage channel, peaty sand, altitude c.15m, 16/11/1992, J. Short, P. Davie. QM W18226, ♂ (13.7mm CL), 1 imm. (7.3mm CL), same locality and physiochemical data as holotype and allotype, in burrows along water line of lagoon. QM W18228, 4♂♂ (12.5-24.9mm CL), ♀ (19.8mm CL), Cape Flattery, 14°59.2'S, 145°18'E, 0.75m, artificial drainage channel, freshwater, peaty sand, water tannin-stained, fringing heathland/rushes, pH 5, hardness 80ppm, 17/11/1992, trapped, J. Short, P. Davie.

COMPARATIVE MATERIAL: *Cherax robustus* Riek, 1951 (from the vicinity of the type locality), QM W15312, 12♂♂ (17.0-30.4mm CL), 5♀♀ (17.9-25.2mm CL), Coonboo Lake, Fraser Is., 25°14'S, 153°10'E, in burrows around periphery of lake, 17/06/1987, S. Brooks, M. Tait.

DESCRIPTION OF HOLOTYPE

Rostrum triangular, dorsally flattened, slightly recurved distally, punctate proximally, glabrous to base of acumen; length c.1.3× breadth (1.6-2.3 in allotype/paratypes), reaching penultimate segment of antennular peduncle (terminal segment in small paratypes); with moderately-developed lateral carinae, carinae commencing in line with postorbital processes, terminating at base of acumen by blunt process (spinose in several paratypes, particularly smaller specimens); ventrolateral margins setose; acumen blunt (acute in allotype/paratypes), setose.

Eyes with cornea large, globular, well pigmented, cystalks slightly concealed by rostrum. Antennula without unique features. Scaphocerite short, length c.1.9× breadth (2.0-2.4 in allotype/paratypes), reaching end of rostrum (slightly exceeding rostrum in allotype/paratypes), broad-

est at mid-length; lamina broadly rounded mesially, lateral margin terminating in well developed spine. Antennal peduncle setose ventrally, coxocerite acute anteriorly (spinate in allotype/paratypes), basicerite laterally spinate.

Carapace punctate, breadth c.0.6×CL, depth c.0.6×CL; postorbital carinae poorly developed, excavated with interconnected punctations, forming irregular sulcus, armed with blunt process

anteriorly (spinate in allotype/paratypes), diverging posteriorly, length c.1/3 cephalon length; cephalon with few tubercles ventrally (absent in small paratypes); branchiostegites slightly inflated, with few indistinct tubercles along cervical groove (spines on allotype/paratypes), granulose anteriorly (non-granulose in smaller paratypes); branchiocardiac grooves distinct (indistinct or absent in paratypes).



FIG.1. *Cherax cartalacoolah* sp.nov., holotype ♂ (30.3mm CL), QM W18224, dorsal view.



FIG.2. *Cherax cartalacoolah* sp.nov., holotype ♂ (30.3mm CL), QM W18224, ventral view.

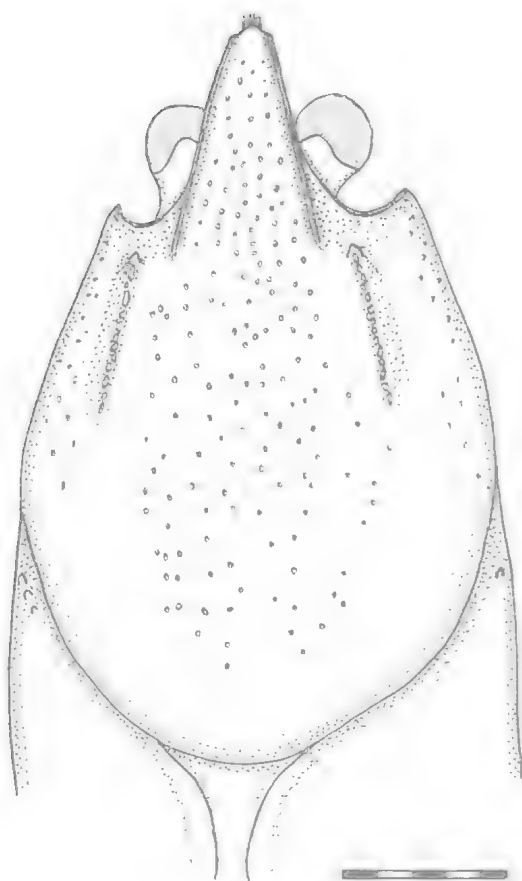


FIG.3. *Cherax cartalacoolah* sp.nov., holotype ♂, QM W18224, anterior carapace and rostrum. Scale divisions in mm.

Epistome slightly concave, sparsely setose, without obvious tubercles, lateral margins entire, slightly crenulate. Mouthparts without unique features. Branchial formula typical for genus (cf. Holthuis, 1949), with posterior arthrobranch above fourth pereopod reduced.

First chelipeds large, subequal (isomorphic in paratypes), distal merus reaching end of scaphocerite (carpus in allotype/paratypes); outer margin of chelae moderately convex; fingers without obvious gape, opposing edges densely setose, bearing low rounded teeth; pollex broad basally; dactylus equal to manus in length; manus moderately broad, breadth equal to length (less than length in paratypes), dorsum moderately-convex longitudinally (slightly convex in allotype/paratypes), strongly convex laterally, mesial margin serrations restricted to proximal half; carpus c.0.3

chela length, bearing large, uncinat mesial spine, blunt process at anteroventral condyle (acute in paratypes), similar process at ventromesial angle followed by two or three tubercles posteromesially, anteromesial angle with dense pubescence of long setae; merus of typical shape, c.0.6 chela length, dorsal carina armed with blunt process (spinat in allotype/paratypes) followed by series of tubercles, ventral surface with pubescence of setae and numerous strong cuticular processes, two or three larger than rest (spinat in allotype/paratypes).

Sternal keel sharp, without spines, lateral processes juxtaposed on T7 and T8, bearing conspicuous pores on T6 and T7. Abdomen punctate, somite 2 pleurae with deep concavity.

COLOURATION

Body colour varying from rusty brown to bluish-grey, ventral manus of first chelipeds magenta to cyanine blue, articular membrane between merus and carpus geranium red.

BIOLOGY

Freshwater, fossorial, burrows terminating slightly below level of water table, supralittoral to shallow littoral areas around perch lakes and along creek banks. Collected from low altitude <15m, peaty sand areas within sand dune formations, generally amongst rushes, fringing heathland. Recorded physiochemical tolerances: pH 5, hardness 40-80ppm, water temperature 33°C, dissolved oxygen 1.7ppm.

DISTRIBUTION

Cape Flattery, northeast Queensland. It is likely, with further collecting, that the range of this species will be extended into other sand dune areas between Cape Bedford and Lookout Point.

ETYMOLOGY

An aboriginal word meaning 'a water hole between two sandhills' (cf. Reed, 1970), which is an accurate description of the type locality. The specific name is to be treated as a noun in apposition.

SYSTEMATIC POSITION

The new species most closely resembles *C. robustus* Riek, 1951, from southeast Queensland, which also occurs in acidic, peaty-sand habitats and has similar colouration. The following morphological features can be used to distinguish the two species:

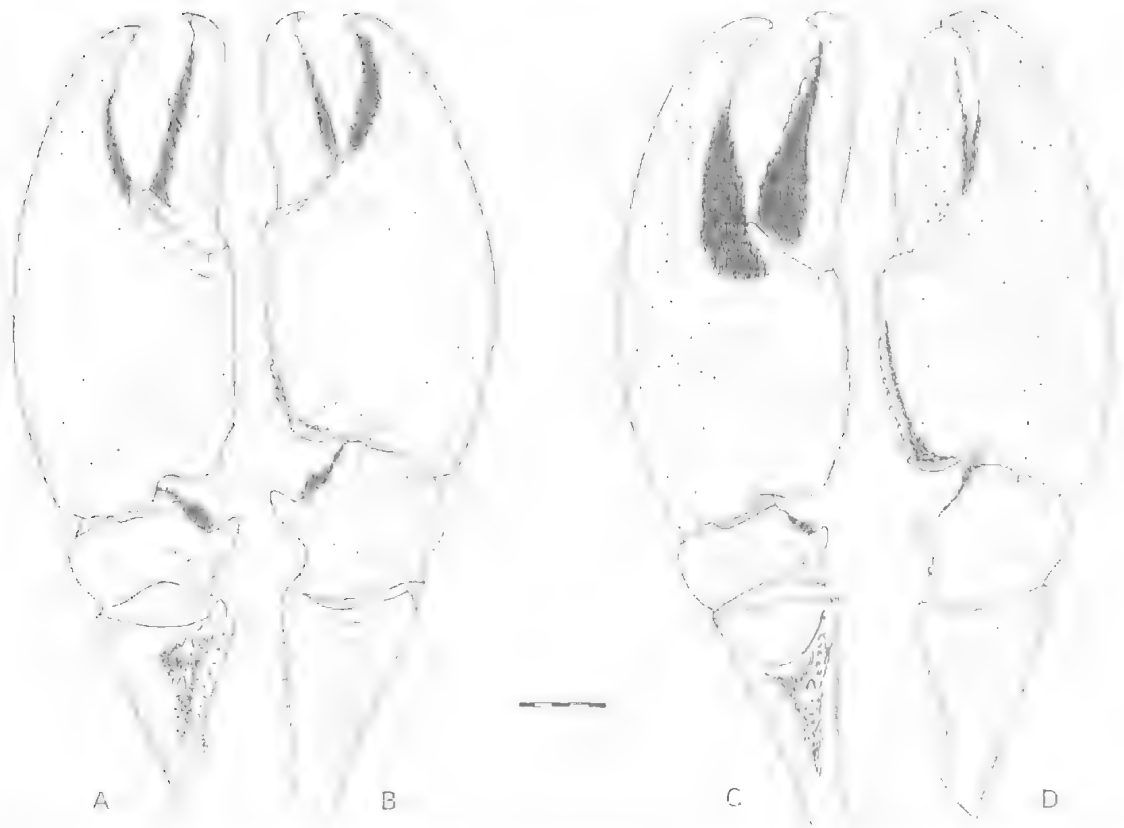


FIG. 4. *Cherax cartalucoolah* sp. nov., holotype ♂, QM W18224: A, ventral view of right first cheliped; B, dorsal view of right first cheliped. *Cherax robustus* Riek, 1951, ♂ (30.2mm CL), QM W15312: C, ventral view of right cheliped; D, dorsal view of right cheliped. Scale divisions in mm.

1. The mesial carpal spine on the first chelipeds is much stouter in *C. robustus* and is usually followed by one or more tubercles. In the present species there are no tubercles behind the spine.

2. The ventral setation on the pollex of the first chelipeds continues for some distance onto the manus in *C. robustus*. In the present species the setation is restricted to the opposing edge of the pollex and does not continue onto the manus.

3. The mesial serrations on the manus of the first chelae continue over about two thirds of the mesial margin length in *C. robustus* whereas in the present species they are restricted to the proximal half.

4. Large adults of the new species have well-developed, branchiocardiac grooves which are lacking in *C. robustus*.

5. The punctations along the postorbital carinae form an irregular sulcus in the present species. In *C. robustus* the punctations sometimes connect anteriorly, but are otherwise well separated.

C. cartalucoolah can easily be separated from nominal species of the 'depressus' group (sensu Riek 1969), which also occur east of the Great Dividing Range in northeast Queensland, by the presence of setal pubescences on the mesial carpus and ventral merus of the first chelipeds.

C. rhynchotus Riek, 1951, which occurs in similar habitats to the new species on northern Cape York Peninsula and Badu Is., Torres Strait, is not a closely allied species and belongs instead to the 'quadricarinatus' species-group (cf. Short, 1991).

ACKNOWLEDGEMENTS

I am grateful to Rolly McKay for bringing this crayfish to my attention. Peter Davie is thanked for allocating QM resources towards the collection of further material, and for his expertise in the field. Des Bolton, Natural Resource Assessments Pty Ltd, kindly organised the assistance of

Cape Flattery Silica Mines Pty Ltd and the Hopevale Aboriginal Community preceding the 1992 collecting trip to Cape Flattery. I am also indebted to John Benfield, Cape Flattery Silica Mines Pty Ltd, for the use of facilities and the assistance of his staff. In particular, Paul Miller provided support and local knowledge during the collecting effort. Mr Steve Brooks donated specimens of *C. robustus* to the QM. Jeffery Wright printed the photographs.

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A RECORD OF COMMUNAL EGG-LAYING IN THE SKINK *CARLIA TETRADACTYLA*. *Memoirs of the Queensland Museum* 33: 60, 1993:- During a visit to the Oakey area, southeast Queensland on 25 November 1992, a communal nest of 25 skink eggs was located. The site — a disused railway line — was approximately 8 km NW of Oakey township and consisted of a relatively continuous row of wooden sleepers.

The nest was located beneath a single sleeper, which was lying on an approximate north-south axis, at its northern end. The whole sleeper was also angled slightly to the west. The eggs varied little in size. All were partially buried in the soil. The eggs were not measured at the time, but their size suggested they could belong to *Carlia tetradactyla*, a very common species at the site. Considering the paucity of records of communal nesting for *Carlia*, one egg was retained by one of us (RP) for artificial incubation to confirm its identification.

On return to Brisbane the egg was transferred to a small plastic container with a little soil from beneath the sleeper and sprayed lightly with water. Access to an incubator was not possible immediately, so the container was maintained between 25–30°C near a 60 watt incandescent light bulb. After two days, the egg had shrivelled markedly and the upper surface had turned a tea-brown colour. However, after a liberal spraying, it almost regained its original shape, though some small wrinkles remained until hatching. After five days the egg was placed in an incubator maintained at 29.5–30.5°C.

On the 3 December 1992, the container was removed from the incubator for the purpose of taking measurements of the egg. However, on opening, it was found the egg had already hatched. Even so, approximate measurements were taken of the empty egg-shell (15.8 × 10 mm). The hatchling was tentatively identified as *C. tetradactyla* and a snout-vent measurement was taken (27.6 mm). It was then transferred to a small holding container where it thrived and began feeding on hatchling locusts within 4–5 days. The specimen was later taken to the Queensland Museum, where its identification was confirmed (P. Couper). It was subsequently lodged as Queensland Museum specimen number J56882.

Considering the consistent clutch size of two eggs for *C. tetradactyla* (Greer, 1989), the large number of eggs found by

us indicates the use of the nesting site by some 13 individual females (or a smaller number of animals laying multiple clutches). Greer states that the communal nests of two genera, *Lampropholis* and *Saproscincus*, usually contain eggs laid almost simultaneously, or at least within a few of hours. He also notes that (at least with the above two genera) nests always consist of eggs from only one species. Thus it seems fair to assume that all 25 eggs belong to *C. tetradactyla*, especially as there were no other abundant, similarly-sized species observed in the vicinity.

Greer (1989) cites only one reference (Wilhoft, 1963) for communal nesting in the genus *Carlia*, *C. rhomboidalis* (= *C. rubrigularis* Ingram & Covacevich, 1989). Thus our record is the second instance of such behaviour in *Carlia*.

It is not known what stimulates several female lizards to lay in the same site. At the nest discovered by us, there did not appear to be any old shells to indicate past use as a favoured nesting site. It is also interesting to speculate why this particular sleeper was chosen amongst hundreds of others. Perhaps it had special features attractive to gravid females, or it may simply have been a choice by one female that, in turn, stimulated several others to lay, possibly by some olfactory cue.

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OCEANAPIA SAGITTARIA FROM THE GULF OF THAILAND

JOHN N.A. HOOPER, MICHELLE KELLY-BORGES AND MARTIN RIDDLE

Hooper, J.N.A., Kelly-Borges, M. & Riddle, M. 1993 06 30: *Oceanapia sagittaria* from the gulf of Thailand. *Memoirs of the Queensland Museum* 33(1): 61-72. Brisbane. ISSN 0079-8835.

Oceanapia sagittaria (Sollas) is redescribed from shallow water, soft benthic communities surrounding the limestone islands of Ko Samui, southwest Gulf of Thailand, with additional new records from southern Papua New Guinea. Morphological redescription is based on live material, highlighting in particular a unique, tentacle-like, dendritic series of exhalant canals with its complex of oscules on the apex of the primary (open) fistule. Evidence is presented to suggest that this capitate structure serves as both a complex series of exhalant pores and canals, and an asexual dispersal propagule. Scanning electron microscope studies also detected an additional morphology of toxa microscleres, not previously recorded for the species, and studies of skeletal structure indicate that the species is more appropriately included in the family Oceanapiidae (Porifera, Demospongiae, Haplosclerida), being the sixth member of the 'biminia' group of *Oceanapia* species. The distribution and comparative morphology of this species group are discussed. □ *Oceanapia sagittaria*, Porifera, Demospongiae, Haplosclerida, Oceanapiidae, Gulf of Thailand, oscular structure, asexual propagule, taxonomy.

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Species of *Oceanapia* are common, with more than 50 nominal species recorded for the Indo-west Pacific region alone, relatively abundant in both soft and hard substrates, and widely distributed (known throughout the world's oceans: Antarctic, ampho-Atlantic, Mediterranean, Red Sea, western and eastern Indian Ocean, Indo-Malay archipelago, Indo-west Pacific, Japan, New Zealand and eastern Pacific Ocean). However, many of these species are poorly known: most *Oceanapia* species have been described only from preserved material; in many cases they have been described only once; in several instances species descriptions are based solely on incomplete individuals (e.g. fistules); and in some cases species were created on the basis of only minor differences in spicule morphometrics from their siblings. These problems are common to many groups of sponges, but possibly they are most apparent in the relatively morphologically depauperate Haplosclerida, including *Oceanapia*. Whilst reexamination of the type material for many of these species is usually necessary (the original descriptions being very brief and/or very poor), generally this process does no more than confirm or refute those characters already described for the species. Consequently, *Oceanapia*

appears to contain many species differing from each other only slightly in any of their major characters (growth form, spicule morphology, spicule size, skeletal structure), whereas in situ observations of live populations are much more informative in discriminating sibling species. In this present paper we redescribe *Oceanapia sagittaria* (Sollas) from live populations in the Gulf of Thailand, including in situ observations of intact capitate, oscular structures peculiar to this species, whereas the species had previously been described only from preserved material (Sollas, 1902; Burton, 1934; Bergquist, 1965), virtually all fragmented. We also describe some observations of populations from southern Papua New Guinea.

METHODS

Preparation of material for light microscopy and scanning electron microscopy (SEM) is described elsewhere (Hooper, 1991). The descriptive language system DELTA was used to prepare the taxonomic description (Dalwitz & Paine, 1986). Abbreviations used in the text are as follows: BMNH, Natural History Museum, London; NCI Q66C-, US National Cancer Institute shal-

low water collection program (Australian Institute of Marine Science, Townsville, contract) – primary material now in Smithsonian Institution, NTM and QM; NMV, Museum of Victoria, Melbourne; NTM, Northern Territory Museum, Darwin; PMBC, Phuket Marine Biology Center, Phuket, Thailand; QM, Queensland Museum, Brisbane; ZMA, Zoological Museum, Amsterdam.

SYSTEMATICS

Family OCEANAPIIDAE van Soest *Oceanapia* Norman, 1869

- Oceanapia* Norman, 1869 [type species: *Desmacidon jeffreysii* Bowerbank, 1866 (= *D. robusta* Bowerbank, 1866 (Carter, 1882))].
Rhizochalina Schmidt, 1870 [type species: *Rhizochalina oleracea* Schmidt, 1870].
Phloeodictyon Carter, 1882 [type species: *Phloeodictyon isodictyiforme* Carter, 1882].
Biminia Wiedenmayer, 1977 [type species: *Oceanapia toxophila* Dendy, 1922].

DIAGNOSIS

Haplosclerida, predominantly fistulose, with a unispicular, tangential, subisotropic ectosomal skeleton, often detachable, and an irregular, longitudinal and/or transverse system of multispicular tracts with a subisotropic reticulation of single spicules dispersed between forming the choanosomal skeleton; microscleres may include sigmas and toxas (modified from de Weerd, 1985).

REMARKS

The genus, its contents, generic synonymy and relationships with other oceanapiids have been discussed at length by several contemporary authors (Bergquist & Warne, 1980; van Soest, 1980; de Weerd, 1985; Wiedenmayer, 1989; Fromont, 1991). The synonymy cited above is now generally accepted, although de Weerd and van Soest (1986) also note that *Rhizochalina* and *Oceanapia* s.s. could be considered two 'convenient' subgenera, differentiated by their consistency and development of their spongin fibre skeletons; the first having strongly developed spongin fibres and the second with a pulpy choanosomal skeleton. However, these apparent differences are not clear-cut for all species (i.e. several species in both nominal genera have intermediate character states), and formal recognition of these 'convenient' subgenera may not be fully justified. In fact, there is equal justification

for recognising alternative 'convenient' subgenera within *Oceanapia*, based on microsclere diversity for example (e.g. *Biminia* with toxas and sigmas, *Oceanapia* (s.s.) with only sigmas, and *Phloeodictyon* (s.s.) without microscleres), but this system also lacks a sound phylogenetic basis (de Weerd and van Soest, 1986).

Oceanapia sagittaria (Sollas) (Figs 1-20)

- Gellus sagittarius* Sollas, 1902: 212, pl.15, fig.7.
Adocia sagittaria, Burton, 1934: 538.
Orinasagittaria, Bergquist, 1965: 155-157, figs 18a-c.

MATERIAL EXAMINED

NTM Z3679, QM G301346, QM G300640, PMBC 9210: E side of northern island, Ko Wao Yai Group Marine National Park, NW of Ko Samui, S Gulf of Thailand, 9°47.0'N, 99°41.0'E, 6 June 1990, 12.5m depth, coll. M. Riddle, S. Sorokin, J.N.A. Hooper, SCUBA (sn JH-90-016). Unregistered material: Motupore I., southern Papua New Guinea, various dates 1987, coll. M. Kelly-Borges.

DISTRIBUTION, SUBSTRATE AND DEPTH RANGE

This species is only recorded from Kepulauan Bidang, north of Penang, Andaman Sea (Sollas, 1902), Ko Samui, southern Gulf of Thailand and Motupore Island, southern Papua New Guinea (present study), Koror I., Palau Islands, central western Pacific (Bergquist, 1965), and the Low Isles, Great Barrier Reef (Burton, 1934). It is probably a widely distributed Indo-Malay species, but because of its small, relatively cryptic, burrowing habit the extent of its distribution is still not fully known. The recorded depth distribution is from shallow subtidal waters to approximately 14m. The Thailand collection site – located 50m from shore, at 12m depth on sand and coral rubble slope, rising to coral dominated slope and *Porites* heads, at base of limestone cliffs rising to greater than 70m altitude – contained a population of this species with many specimens, although the species was not seen in any other sites in this region. In southern Papua New Guinea the species is also relatively abundant, found in muddy silt substrates.

DESCRIPTION

Shape. Sponge burrowing into soft sediments; slightly enlarged basal root submerged completely below substrate, with one or more fistules protruding above surface (Fig. 1). Basal root (or 'body' of sponge) expanded, bulbous, subspheri-



FIG. 1. *Oceanapia sagittaria* (specimen NTM Z3679) in situ (photo M.Riddle).

cal, more-or-less solid, attached to detritus in soft sediments (Fig. 6). All collected specimens consisted only of single primary fistules, with or without smaller, vestigial, secondary (blind) fistules, erect on single basal roots; primary fistule cylindrical, tubular, hollow, with cavernous central lumen, widest at base, tapering to constriction below apex; fistules simple-flagelliform, flexible, fleshy, mucous-covered in life, although more fragile, thin-walled when preserved. Apex

of primary fistule with unusual capitate structure (= capitum), which in life is extremely fragile, subspherical, membranous on its exterior surface, completely translucent, clearly showing dendritic fibre and canal system within (Fig. 1); membranous capitum collapses upon collection, leaving only dendritic fibres and spicule tracts, tapering at their ends (Figs 7,8). Dimensions: basal root 11-23mm diameter; primary (open) fistule 33-54mm long, 2-4.5mm external diameter, 1.5-4.0mm internal diameter; secondary (blind) fistules 8-18mm long, up to 2.5mm external diameter; capitum (in life, when intact) approximately 20mm diameter, when preserved (i.e. dendritic fibres situated on apex of fistule) 7-11mm long, 4-10mm wide. Growth form consistent for all known specimens.

Colour. Live colouration of basal root dark brown or black; fistules dark red-brown (Munsell 5R 4/10); fibre bundles inside translucent capitum pale red in life (2.5R 6/10) (Fig. 1). Live colouration relatively consistent. Colour of specimens in ethanol grey-brown.

Oscules. Oscules confined to distinct areas on membranous capitum at apex of sponge; terminal, situated at the ends of dendritic fibre bundles (which probably surround/support exhalant canals), protruding from apex of sponge (Fig. 6); primary fibre bundles thickest at centre of capitum, bifurcating only once or twice within membranous capitum, with each exhalant canal slightly swollen at apex, and each bearing a single oscule; oscules more-or-less evenly distributed

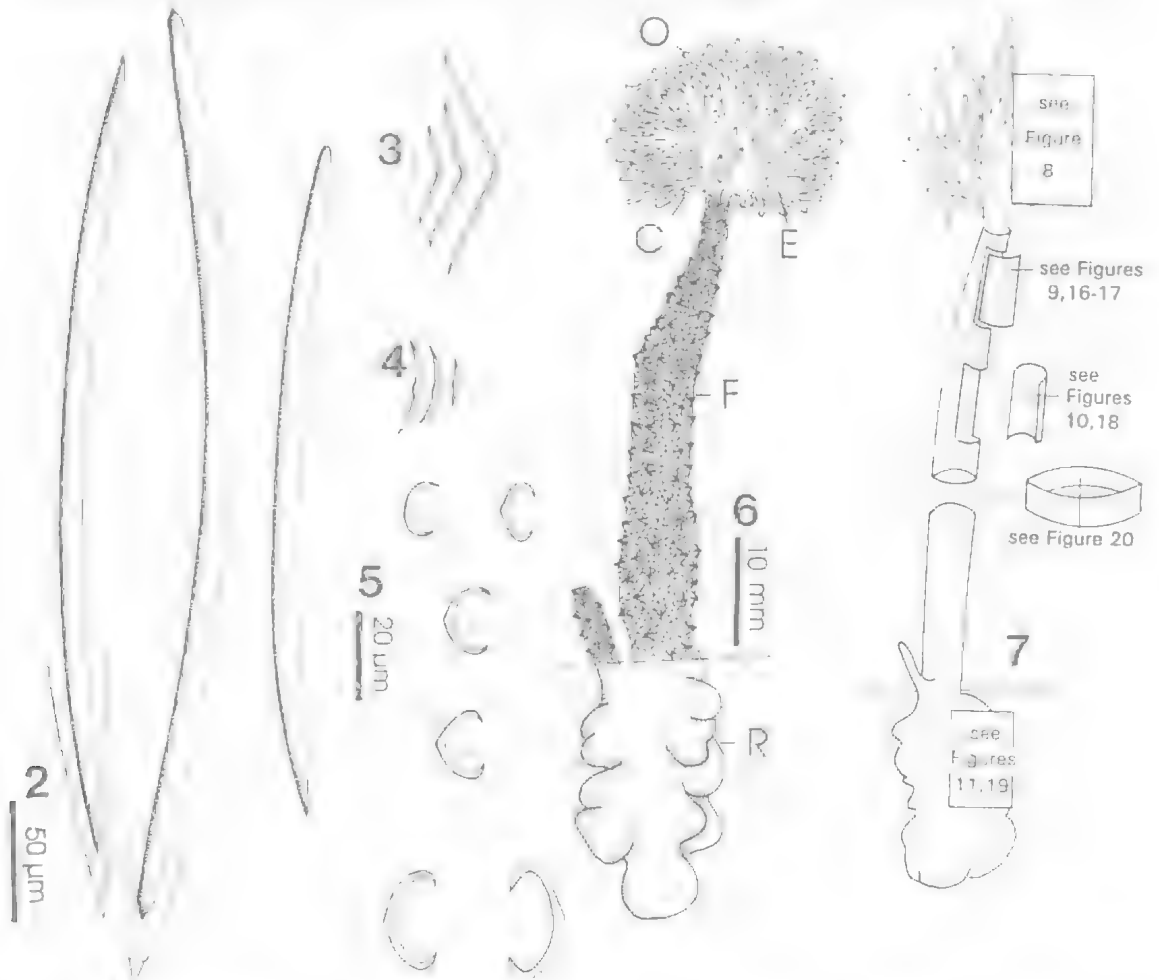
over entire capitum, minute, 0.2-0.5mm diameter, but not observable in preserved material (i.e. capitum collapses). Inhalant pores not seen.

Texture. Fistule soft, elastic, flexible, fragile, easily torn both in life and when preserved; basal root solid, woody, inflexible, easily crumbled.

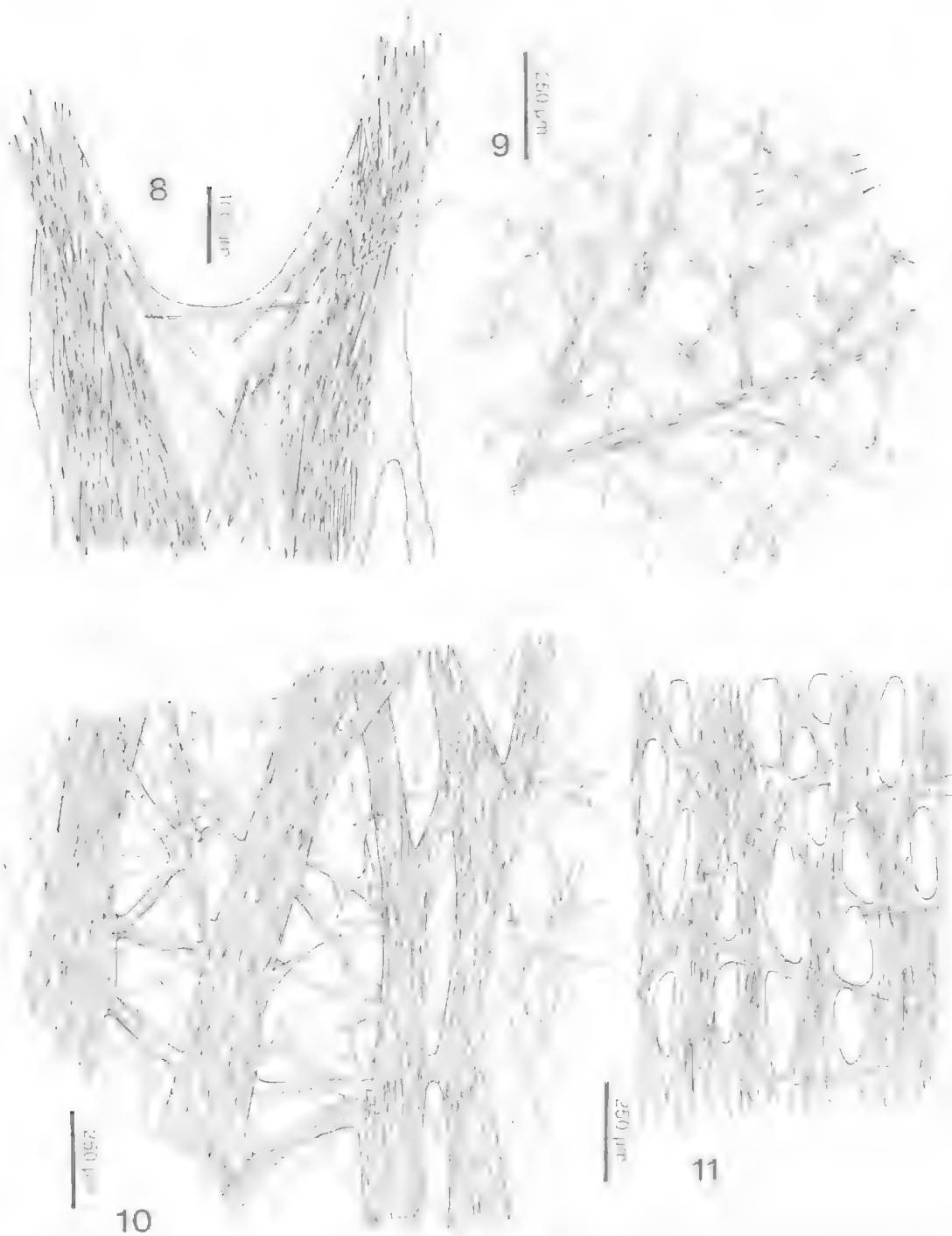
Surface characteristics. Fistule fleshy, collagenous, pigmented, microconulose, prominently sculptured in life (Fig. 6), with prominent tangential spicule skeleton forming a microscopic, triangular, cobweb-like network (Figs 9, 16-17), although appearing more shaggy when preserved. Membranous capitum skin-like,

glabrous in life, with faint, fragile, irregularly isodictyal, tangential spicule skeleton; capitum is translucent in life and choanosomal fibres clearly visible through membranous surface. Basal root dense, spiculose, heavily pigmented, with smooth surface, and loose, irregular, tangential spicule skeleton, although the latter is not a prominent feature.

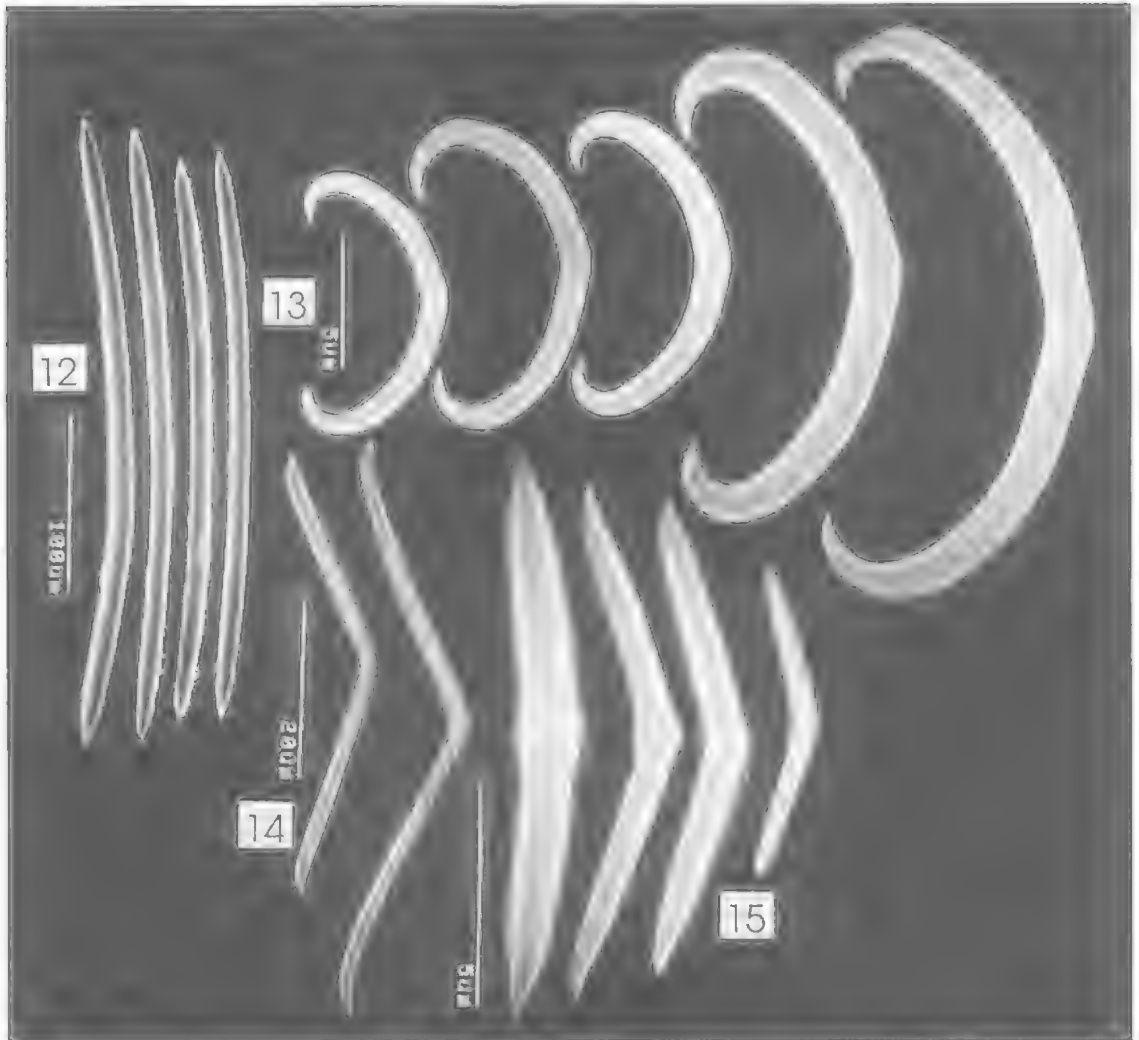
Ectosome and subectosome. Ectosomal skeleton with both unispicular and paucispicular tangential tracts of oxeads (Figs 9, 17). Capitum, when intact, with unispicular, subisodictyal, tangential ectosomal tracts, without any support underlying



FIGS 2-7. *Oceanapia sagittaria*, spiculation and morphology. 2, oxeads (and rare anisoxeads). 3, long toxas. 4, robust, centrangulate toxas. 5, centrangulate sigmas. 6-7, interpretation of live, whole specimen (from Fig. 1), with stippled basal region indicated below substrate. 7, guide to location of sections depicted in figures 8-20. F=tubular fistule, C=membranous capitum, R=basal root, with woody exterior and pulpy interior, O=osculum, E=exhalant canal.



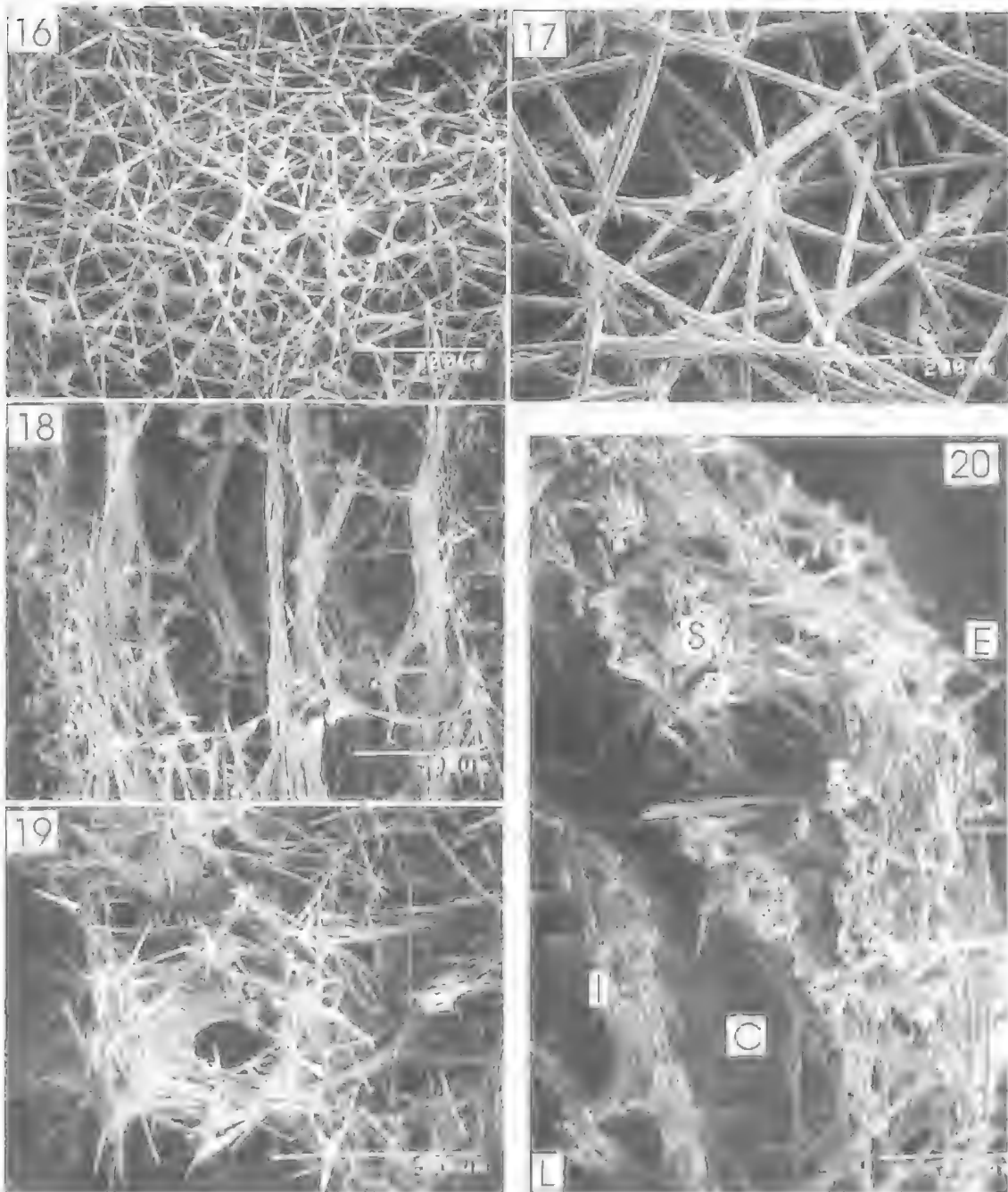
FIGS 8-11. *Oceanapia sagittaria*, interpretation of regional skeletal structures. 8, tip of capitum in preserved condition, showing ascending spicule bundles supporting individual exhalant canals (oseules collapsed). 9, external wall of fistule, showing unispicular, isotropic overlying skeleton and multispicular supporting tracts of subectosome. 10, internal wall of fistule, showing multispicular choanosomal tracts, interspersed with unispicular, isotropic spicules. 11, section through basal root (or 'body' of sponge, burrowing into substrate), with reticulate, pulpy architecture.



FIGS 12-15. *Oceanapia sagittaria*, scanning electron micrographs of spicules. 12, oxeas. 13, centrangulate sigmas. 14, long toxas. 15, robust, centrangulate toxas.

ectosomal skeleton (unlike most other parts of the skeleton). Fistule with both uni- and paucispicular tracts of oxeas tangential to surface, with multispicular tracts visible just below surface (Fig. 9), and a prominent cavernous area between ectosomal (unispicular and paucispicular) and choanosomal (multispicular) regions (Fig. 20). Basal root with dense, disorganised, unispicular, tangential tracts and dense, multispicular, tracts below the ectosome (Fig. 19), both close to surface. Extra-fibre spicules (i.e. those not associated with the tangential unispicular ectosomal or multispicular subectosomal skeletons) lie in sparse, single or paucispicular subisodictyal tracts throughout the skeleton (Fig. 10).

Choanosome. Choanosomal skeletal structure reticulate, composed of relatively homogenous, dense spicule tracts differentiated into primary (longitudinal) and secondary (transverse) skeletal lines. Primary tracts long, multispicular, 70-160 μm diameter, joined by shorter pauci- or multispicular secondary tracts, 30-50 μm diameter, together forming irregular elongate or elliptical meshes, 450-1500 μm long, 120-250 μm wide. Extra-fibre spicules scattered between choanosomal meshes, in unispicular, subisodictyal tracts. Basal root ('body' of sponge), pulpy, occupying most of 'body' diameter, with central lumen of fistules extending several millimetres into 'body', and with large, cavernous meshes pro-



FIGS 16-20. *Oceanapia sagittaria*, scanning electron micrographs of skeletal structure (see Fig. 7 for location of sections). 16, tangential, unispicular, isotropic reticulation of ectosome, exterior wall of fistule. 17, close-up of same. 18, multispicular, mostly longitudinal reticulation of interior wall of fistule. 19, cavernous, pulpy choanosomal skeleton of basal root ('body' of sponge). 20, cross section through fistule wall, showing exterior unispicular tracts (E), with subectosomal support (S), a cavernous region in between (C), interior multispicular tracts of choanosome (I) lining lumen of fistule (L).

duced by reticulation of longitudinal and transverse skeletal tracts, up to 0.5mm diameter (Figs 11,19). Fistules with greatly compressed choanosomal skeleton, attached directly to the interior of fistule walls (Figs 10,18). Spongin fibre skeleton greatly reduced; spongin fibres typically very light (Figs 10,11), whereas spicules between major tracts (i.e. forming the subsodictyal skeleton) usually bound together by sparse, granular, lightly pigmented collagen. Collagen in mesohyl abundant, darkly pigmented, dispersed evenly throughout, slightly granular, packed with microscleres. Choanocyte chambers minute, ovoid, 12-26µm diameter, lined by sigma and toxa microscleres.

Megascleres. Relatively long, thin, smooth oxeas (Figs 2,12), slightly curved, with fusiform points or occasionally slightly constricted near apex and bearing a sharp, mucronate, abrupt point; very homogenous in size throughout skeleton (length 329-363.4-393µm; width 9-10.8-12µm).

Microscleres. Two categories of microscleres present, both very abundant. C-sigmas (Figs 5,13), of a single size class, varying only slightly in size, usually very small, thin, typically centrangulate, never s-shaped or contort, completely smooth (length 8-12.6-22µm, width 0.5-1.2-2µm).

Toxas include two morphs, the larger more common: (i) long, thin, v-shaped toxas (Figs 3,14), with wide angular central curvature, and reflexed points (at extremities only) (length 28-41.9-68µm; width 0.5-1.2-2.5µm); (ii) short, thin, robust toxas (Figs 4,15), with only slight angular central curvature and slightly swollen (centrangulate) at centre, and with straight (unreflexed) points (length 8-13.7-23µm; width 0.5-1.2-1.5µm).

In situ observations. Field and laboratory observations were made over a period of several weeks in 1987 (M.K.B.). In the field, the capitum is easily dislodged from the apex of the fistule with only moderate movement of the water column above the specimen. Several dislodged capitulate structures were observed lying on sand, in coral reef interstices and seagrass beds in the vicinity of Motupore Island. Laboratory observations on several intact specimens suggest that the capitum may have an asexual reproductive function. Several observations were made: 1, several capitulate structures were carefully detached from transplanted aquarium specimens, through gentle movement of the water column directly above specimens. After detachment, capitulate structures

rolled over the aquarium floor until they became wedged in substrate; 2, after 24 hours of resting on the substrate the dendritic exhalant canal tubes, easily visible within the capitum (Fig. 1), extended towards and became attached to the substrate, forming a plate-like, basal, anchoring structure; 3, 36-48 hours after detachment these spherical capitulate structures deflated, slightly flattened at the apex, and spread laterally into a thickened plate with single apical oscule.

Field observations in the Gulf of Thailand (J.N.A.H. and M.R.) also noted that these capitulate structures are elaborate exhalant devices. Small particles of silt and other detritus were observed to be periodically expelled from the small oscules scattered over the capitum. Ostia (inhalant pores) were not seen.

REMARKS

Oceanapia sagittaria is unique amongst all oceanapiids (in fact, as far as known, amongst all sponges), in having the peculiar capitulate structure on the apex of its primary fistule. Bergquist (1965: 155) first hypothesised that these 'terminal caps', apparently observed free floating in the Palau Islands, might be asexual dispersal mechanisms. We confirm this idea in the present study, and suggest that this structure is the first documented case of a specialised asexual propagule recorded for the Haplosclerida, although many cases of 'unspecialised' surface and basal buds are known for several Hadromerida (e.g. *Polymastia* (Battershill & Bergquist, 1990), *Tethys* (Bergquist & Kelly-Borges, 1991), *Aaptos* (Bergquist, 1968)).

The holotype of *O. sagittaria* was apparently originally deposited in the Zoological Museum at Cambridge University, but this material has not been mentioned since Sollas's (1902) publication and it is unknown if it still survives. A spicule preparation of the holotype is also apparently located in the Natural History Museum, London (BMNH 1938.8.7.3), but this preparation contains no details of skeletal structure (F. Wiedenmayer, pers.comm.). Although *O. sagittaria* has now been described from three separate collections, only the description of Bergquist (1965), based on preserved material, is adequate by modern standards. Sollas (1902) provided an extremely brief description, essentially only describing spicule shape and size, without any useful information on skeletal structure. Oxeas were cited as 300-350×10-13µm, sigmas 12-16µm long, and toxas were 49µm long. Burton (1934) did not provide any details of the Great

Barrier Reef material, but merely compared his and Sollas's fragments. Bergquist's (1965) more detailed description of Palau Islands specimens gave spicule measurements as: oxeas (325-375 \times 5.5-10 μ m), centrangulate sigmas (10.5-20.5 μ m long), and toxas (36-50 μ m long). These dimensions, compared to those seen in the Gulf of Thailand specimens, indicate that the species is relatively homogeneous across its range, although live colouration differs slightly: Burton (1934) reported that Great Barrier Reef material was magenta and ultramarine, whereas both the present specimens and those described by Bergquist (1965) were simply red-brown or bright red, respectively.

Oceanapia sagittaria has been previously included with the family Chalinidae Gray (or its synonym Adociidae de Laubenfels), whereas it is clearly a member of the Oceanapiidae and consequently defined in this family in the present study. The Chalinidae have a more-or-less regular, unilayered, unispicular, isotropic, tangential ectosomal skeleton, with three-sided spicule meshes. In *Oceanapia* this peripheral skeleton may also be regular, isodictyal, with vaguely triangular meshes, but the tangential layer of spicules is substantially more dense and the nodal spongin, prominent in many species of Chalinidae, is usually absent (Fig. 16). Similarly, choanosomal structure in the Chalinidae is ladder-like, with uni-, pauci- or multispicular tracts, whereas in *Oceanapia* primary ascending fibres are multispicular, supporting the dense tangential ectosomal skeleton, and supplemented by a secondary (isotropic) reticulation of single spicules lying between the main fibres (Figs 10, 11, 13) (de Weerd, 1985).

In the strict sense, the present species belongs to the nominal genus *Biminia*, in having both centrangulate sigmas and toxas microscleres in a fistulose, reinforced oceanapiid skeleton. However, de Weerd (1985) and de Weerd & van Soest (1986) argue that these microscleres may represent the retention of a primitive character and hence not valid at the generic level. They suggest that the genus should be dropped into synonymy with *Oceanapia* as the two nominal genera are virtually identical in all other respects. Several other haplosclerids have both sigma and toxas microscleres, including species of Chalinidae (e.g. *Orina*) and Callyspongiidae (e.g. *Callyspongia*). *Orina* lacks the distinctive pulpy, reinforced, multispicular choanosomal skeleton of *Oceanapia*, having instead a unispicular, isotropic choanosome, and *Callyspongia* has a dis-

tinctive network of tangential primary, secondary, and occasionally tertiary fibres in the ectosomal skeleton, and typically regularly reticulate, wide-meshed, choanosomal fibres cored by single or few spicules. Both Burton (1934) and Wiedenmayer (1977) discuss examples of this convergence between *Oceanapia* (as *Biminia*), *Orina* and *Callyspongia* further.

An alternative point of view, offered by de Weerd & van Soest (1986), is that the distribution of 'biminias' may reflect a possible Tethyan distribution of their common ancestor, although they are sceptical about whether this combination of characters is an apomorphy for *Oceanapia* [as inferred by Wiedenmayer (1977) and Hooper (1984)], or whether it is a synplesiomorphy and thus contains no phylogenetic information [as proposed by van Soest (1980)]. Further analysis of this possibly ancestral, possibly Tethyan distribution should be made by comparing the distributions of both the 'biminia' and non-biminid groups of *Oceanapia*, and the comparative distributions of the *Orina* and *Reniera* groups of Chalinidae. However, much of the type material relevant to this analysis, presently unavailable, firstly requires re-examination.

In addition to *O. sagittaria* there are five other species of *Oceanapia* that fit in the 'biminia' group: *Oceanapia toxophila* Dendy, 1922:45 from Providence I., Seychelles Is., western Indian Ocean (holotype BMNH 1921.11.7.37 re-examined); *O. stalagmitis* (Wiedenmayer, 1977:124) from the Bahamas; *O. ooita* (Hoshino, 1981:122) from Japan; *O. macrotoxa* (Hooper, 1984:55) from the Timor and Arafura Seas, northwest Australia (holotype NMV F51373); and *O. cancap* de Weerd & van Soest, 1986:39 from the Madeira region, West Africa, southeast North Atlantic. In addition to these taxa, re-examination of Ridley's (1884:424) material of '*Gellius fibulatus*' from Torres Strait, Qld (BMNH 1822.2.23.281) found that it is neither a chalinid nor conspecific with *Reniera fibulata* Schmidt, 1862, but belongs to Oceanapiidae and furthermore appears to be identical to *O. macrotoxa*. The identity of an Indonesian specimen collected by the Siboga expedition (ZMA POR 1709), cited as *O. toxophila* by de Weerd (1985:81), is not certain, but it too is possibly conspecific with *O. macrotoxa*. An alternative point of view is that these three nominal Indo-west Pacific 'biminia' species, *O. toxophila*, *O. macrotoxa* and *O. ooita*, may be geographic variants of a single, widely distributed species, extending from the Seychelles Islands to Japan, Indonesia, northwest and northeast Australia,

Apart from the peculiar capitum seen in *O. sagittaria*, there are few major differences between any of the 'biminia' species in external morphology, skeletal structure, spicule geometry or spicule size (as noted by Hooper, 1984: table 1). Thus, it would be equally justifiable to synonymise all six known 'biminia' species as it would be to combine the three Indo-west Pacific species on the basis of these conventional morphometric characters. For the present we maintain all these species in the 'biminia' group, but recognise that only more comprehensive collections of *Oceanapia* throughout the Indo-Pacific may discover material with intermediate characteristics, resolving present doubts.

Apart from the peculiar capitum, *O. sagittaria* is most similar to *O. toxophila*. However, oxeas are sharply pointed, fusiform, or occasionally mucronate in the present species, whereas in *O. toxophila* they are hastate or rounded; oxea size is relatively homogeneous within both species but substantially larger in *O. sagittaria*; microsclele dimensions are similar in both species (see dimensions below for *O. toxophila*), although *O. toxophila* has both c-shaped and contort sigmas, and *O. sagittaria* was discovered to have a morphologically distinct, smaller category of centrangulate, robust toxas, not previously described for the species. Although these differences in spicule size and geometry could be construed as being relatively trivial, they are certainly as substantial as any of the differences between all other 'biminia' species.

Morphological characteristics of other 'biminia' species are as follows. *Oceanapia toxophila* Dendy has a tubular, burrowing, globular, simple base, with very thin, single fistules on each end of the body (the larger, open fistule is apical, the smaller, blind fistule is a basal rootlet); fistules up to 50mm long, 5mm diameter; ectosomal skeleton is a detachable, thin, unispicular, subisodictyal crust; choanosomal skeleton contains both reticulate, multispicular bands and a dense feltwork of subisodictyal spicules; oxeas hastate or rounded, mostly blunt (265-315×5-12µm); microscleles are only moderately common; sigmas very small, c-shaped or contort (12-26×0.5-1.5µm); toxas sharply angular at centre, straight arms, slightly reflexed points (12-55×0.5-2.5µm) (redescribed from the holotype BMNH 1921.11.7.37 (RN XX.2) and Dendy (1922) in part).

Oceanapia stalagmitis (Wiedenmayer) has a semi-incrusting, burrowing, massive base, with multiple, short, open and blind fistules on upper surface, rhizome-like blind fistules on under sur-

face; fistules up to 17mm long, 10mm diameter; ectosomal skeleton a dense, subisodictyal, unispicular layer over a denser detachable crust; choanosomal skeleton an irregular reticulation of both stout and thin fibres, with unispicular subisodictyal spicules dispersed between; oxeas usually sharply pointed, fusiform (100-155×3.5-5µm); microscleles abundant; sigmas centrangulate, c-shaped (11-32×0.5-1µm); toxas small, slight central curvature, straight arms, very slightly reflexed points (10-32×0.5-1µm) (Wiedenmayer, 1977).

Oceanapia ooita (Hoshino) has a massive, subspherical, burrowing base, with numerous, open, wide fistules on upper surface, and rhizome-like, blind fistules on under surface; fistules up to 40mm long, 8mm diameter; ectosomal skeleton dense, unispicular, subisodictyal; choanosomal skeleton with densely packed, longitudinal spicule tracts, interdispersed with subisodictyal single spicules; oxeas homogenous, abruptly pointed, hastate (180-218×7-9µm); microscleles abundant; sigmas c-shaped, centrangulate (14-35µm up to 1µm); toxas slightly curved at centre, straight arms, straight points (up to 45µm, thin) (Hoshino, 1981).

Oceanapia macrotaxa (Hooper) has a burrowing, massive, subspherical base with many long, thin, open and blind fistules on the upper surface, and smaller, thinner, rhizome-like blind fistules (rootlets) on the under surface; fistules are up to 60mm long, 8mm diameter; ectosomal skeleton is a thick, detachable, unispicular, subisodictyal crust; choanosomal skeleton with multispicular tracts, some ascending as well as uni- or paucispicular, subisodictyal tracts dispersed between; oxeas are divided into two indistinct size classes, fusiform to subhastate, mostly sharply pointed (94-260×1.5-7µm, 171-279×6-11µm); microscleles abundant; sigmas are small, centrangulate, c-shaped (9-35×0.5-2.0µm); toxas have angular central curves, straight arms and reflexed points (8-82×0.4-3.5µm) (Hooper, 1984).

Oceanapia cancap de Weerd and van Soest is burrowing, fistulose, although the base is unknown; fistules are open, single or bifurcate, up to 80mm long, (?) 50mm diameter; ectosomal skeleton unispicular, tangential, subisodictyal; choanosomal skeleton (only known for fistule walls) is longitudinal, branching and anastomosing, multispicular tracts with interdispersed subisodictyal single spicules; oxeas fusiform, sharply pointed (up to 320×8µm); sigmas c-

shaped, centrangulate (20µm, thin); toxas with slight central curvature, straight arms, slightly reflexed points (50-75µm, thin) (de Weerd and van Soest, 1986).

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A NEW SPECIES OF *NYCTIMYSTES* (ANURA: HYLIDAE) FROM THE STAR MOUNTAINS, PAPUA NEW GUINEA

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Richards, S.J. & Johnston, G.R. 1993 06 30: A new species of *Nyctimystes* (Anura: Hylidae) from the Star Mountains, Papua New Guinea. *Memoirs of the Queensland Museum* 33(1): 73-76. Brisbane. ISSN 0079-8835.

Nyctimystes oktediensis sp.nov. is a member of the *N. papua* group. Morphologically, it is similar to *N. disrupta* from which it can be distinguished by its brown iris, reduced finger webbing, and palpebral venation of vertical to oblique lines over most of the eyelid. *N. oktediensis* is a stream-dwelling species inhabiting lower montane rainforests in the rugged Ok Tedi headwaters region of western Papua New Guinea. □ *Hylidae, Nyctimystes oktediensis*, new species, Papua New Guinea.

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The montane hylid genus *Nyctimystes* is characterised by the presence of vertical pupils and palpebral venation (Zweifel, 1958). Twenty-three species are presently known, with 21 from the island of New Guinea (Zweifel, 1958; 1983), one species in northern Queensland, Australia (Czechura, Ingram & Liem, 1987) and another in the Moluccas.

Within *Nyctimystes* a distinctive, and presumably monophyletic, group of species has been referred to as the *N. papua* species group (Zweifel, 1983). Members of this group are moderate to large in size, have sparse or much reduced palpebral venation, lack a vocal sac in males, have short, high, rounded snouts, and the outer fingers are no more than one half webbed. Although Zweifel (1983) recognised only four species in the group, he was aware of several specimens that could not be allocated to any known species.

In November 1991, we surveyed the frog fauna of the upper Ok Tedi drainage basin on the southern slopes of the Star Mountains, central New Guinea. We collected 36 species, of which almost one half could not be allocated to any known taxon. The only *Nyctimystes* that we encountered was an undescribed member of the *N. papua* group. Our specimens were most similar morphologically to *N. disrupta* but had a brown iris, reduced webbing between the fingers, and less disrupted palpebral venation.

Measurements and terminology follow Zweifel (1983). Abbreviations used in the text are: SV, body length from snout to vent; TL, tibia length; FT, foot length; HD, hand length; EN, eye to naris distance; IN, internarial distance; SN, snout to

naris distance; HW, head width; EY, eye diameter.

Specimens are housed in the Queensland Museum (QM), South Australian Museum (SAM), Biology Department, University of Papua New Guinea (UP) and the American Museum of Natural History (AMNH).

Nyctimystes oktediensis sp.nov.
(Figs 1-3)

MATERIAL EXAMINED

HOLOTYPE: QM J56896 adult male with nuptial pads, collected by S.J. Richards & G.R. Johnston at 1625m, 23 November 1991 on the southeastern slopes of Mt Akrik, Star Mountains, Western Province, Papua New Guinea (5°10'S, 141°10'E).

PARATYPES: QM J56897-8, SAM R40771 three adult males with nuptial pads, same data as holotype but collected on November 24, 1991; UP 5137-9, three adult males with nuptial pads collected by D. Hyndman, 16 February 1975, from a stream adjacent to the Bleil Bil hunting lodge at Kamfon (2200m), Kam Valley, Star Mountains, Western Province, Papua New Guinea.

DIAGNOSIS

Nyctimystes oktediensis is distinguished from its congeners by a combination of the following characters: palpebral pigmentation relatively sparse; males without vocal sac; iris brown in life; fingers less than half webbed; tympanum indistinct but visible; moderately large size (males 60.8-67.2mm SV).

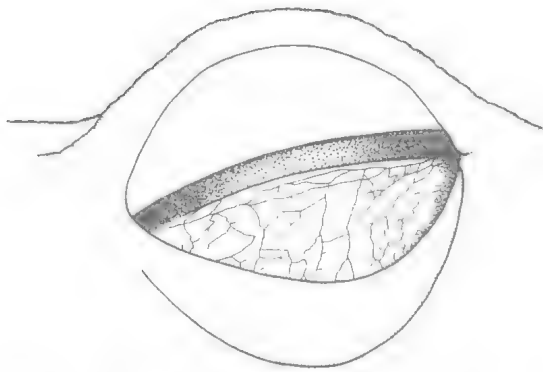


FIG. 1. Right eye of *Nyctimystes oktediensis* (holotype) showing palpebral venation.

DESCRIPTION OF HOLOTYPE

Adult male with the following measurements and proportions: SV 60.8; TL 35.8; HW 21.8; EY 7.8; EN 5.0; IN 6.5; SN 3.5; HD 24.0; FT 32.1; width of third finger disc 4.4, width of third penultimate phalanx 2.7; width of fourth toe disc 3.8, width of fourth penultimate phalanx 3.0; TL/SV 0.588; HW/SV 0.358; EN/SV 0.082; EY/SV 0.128; IN/SV 0.106; EN/IN 0.769.

Snout short, high, rounded in dorsal view, almost vertical in lateral view; canthus rostralis distinct, slightly curved; loreal region steep, slightly concave; nostrils directed laterally (quite evident in dorsal aspect), internarial distance distinctly greater than distance from eye to naris (EN/IN 0.769). Pupil vertical. Palpebral pigmentation of vertical to oblique lines over entire eyelid, with few broken, interconnecting horizontal lines, slightly weaker posteriorly (Fig. 1). Tympanum indistinct but visible, dorsal one quarter of tympanic annulus hidden by postocular fold. Vocal sac absent. Vomerine teeth in two transverse rows between the internal nares.

Relative lengths of fingers 3>4>2>1; scanty webbing between third and fourth fingers, reaching halfway to distal subarticular tubercle on fourth, and to proximal tubercle on third; subarticular tubercles single; disc of third finger more than half eye diameter. A finely granular nuptial rugosity on inside of first finger. Relative lengths of toes 4>5=3>2>1, webbing almost to discs on all toes except fourth, fourth toe webbed to just short of distal subarticular tubercle; subarticular tubercles rounded, single; a low, oval inner metatarsal tubercle but no outer one (Fig. 2).

Dorsal surfaces slightly rugose, without conical asperities. A strong fold from posterior corner of eye to above arm insertion. Ventral surfaces granular. No heel lappet. Dorsally olive green.

Lateral surfaces mottled olive gold and dark brown. Limbs and back (posteriorly) with a mosaic of olive green patches edged with dark brown, and interspersed with olive gold tending to form bands across the limbs. Venter speckled with cream and grey, iris brown (Fig. 3).

VARIATION

The smallest specimen, the holotype, has more widely spaced nares than the paratypes (EN/IN 0.769 vs 0.800-1.00). While the palpebral venation is similar in all of the type series, there is some variation in the degree to which the oblique lines are interconnected horizontally, and the venation of one specimen (QM J56898) is scarcely detectable on the posterior one quarter of the right eyelid (clearly visible on left eyelid). Proportions of the paratypes are as follows: TL/SV 0.583-0.627; HW/SV 0.342-0.356; EN/SV 0.080-0.087; EY/SV 0.110-0.127; IN/SV 0.082-0.100; EN/IN 0.800-1.00.

COMPARISON WITH OTHER SPECIES

The reduced palpebral venation, lack of a vocal sac, snout shape, basal finger webbing and size of *N. oktediensis* show that it is a member of the *papua* group defined by Zweifel (1983). However, *N. papua* is a much smaller species, with females smaller or about the same size as male *N. oktediensis*, and has only a few flecks of black pigment in the anterior corner of the lower eyelid (Menzies, 1975; Zweifel, 1983). Even allowing for greater variation when additional specimens are collected (see Zweifel, 1983), palpebral venation of this species is unlikely to approach the state of *N. oktediensis*. *N. trachydermis* is larger than *N. oktediensis* (smallest male *N. trachyder-*



FIG. 2. Left hand (a) and foot (b) of *Nyctimystes oktediensis* (holotype) in palmar and plantar view respectively.



FIG. 3. Holotype of *Nyctimystes oktediensis* in life.

mis 71.6mm), has conical asperities on the dorsum, and a completely concealed tympanum. The sole specimen of *N. tyleri* (a male) is also much larger (78mm), and had a bright yellow iris (brown in *N. oktediensis*) in life (Zweifel, 1983). *N. disrupta* is similar in size to *N. oktediensis* but has a green iris in life, more extensive webbing between the fingers, and palpebral venation of very fine, disrupted lines (Zweifel, 1983).

HABITS AND HABITAT

The Mt Akrik specimens were collected at night from branches overhanging the Ok Kun, a steep rainforest stream draining into the Ok Tedi. None

was heard calling, and additional observations are required to determine whether this species can vocalise. At least four species of suctorial tadpoles were collected at this site, but we are unable to associate any of these positively with *N. oktediensis*.

DISTRIBUTION

Currently known only from the Star Mountains in central New Guinea.

ETYMOLOGY

Named for the rugged upper Ok Tedi drainage basin where all of the types were collected.

REMARKS

Zweifel (1983) discussed several samples of *N. disrupta*-like specimens that he was unwilling to assign to any known taxon. All of these have finger webbing typical of *N. oktediensis* but most show characters distinguishing them from this species. Two specimens from Irian Jaya (AMNH 49671, 49674) are quite distorted, making accurate measurements impossible, and we are unwilling to assign these to *N. oktediensis* without fresh material. An adult male from Telefomin (AMNH 114817) agrees well with the type series, although the colour of the iris in life is unknown, and we tentatively assign this specimen to *N. oktediensis*. Specimens from Okefomin (AMNH 11485-6), Ialibu (AMNH 81025-6), and Wagau (AMNH 74816-7) have much less palpebral venation than *N. oktediensis*. A series of adult males from Nipa, Southern Highlands (AMNH 103184-8) are large (to 72mm), extremely rugose dorsally (but without conical asperities), and have a completely hidden tympanum. They clearly represent a species distinct from *N. oktediensis* and all other described *Nyctimystes*.

Hyndman & Menzies (1990) list two unassigned species of the *Nyctimystes papua* group from the Ok Tedi region. Their *N. (?) papua* (UP 6719) possesses a vocal sac and thus is not a member of this group. The specimens listed as *N. cf. disrupta* (UP5137-9) agree with *N. oktediensis* in all respects, and are included in the type series.

ACKNOWLEDGEMENTS

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THE TAXONOMY AND DISTRIBUTION OF *PETAURUS GRACILIS*
(MARSUPIALIA: PETAURIDAE), WITH NOTES ON ITS ECOLOGY AND
CONSERVATION STATUS

STEVE VAN DYCK

Van Dyck, S. 1993 06 30: The taxonomy and distribution of *Petaurus gracilis* (Marsupialia: Petauridae), with notes on its ecology and conservation status. *Memoirs of the Queensland Museum* 33(1): 77-122. Brisbane. ISSN 0079-8835.

Petaurus gracilis is morphologically and biochemically distinct from *P. norfolcensis* from which it is geographically isolated. Since its description in 1883, *P. gracilis* has been recorded from 22 localities between Ingham and Tully (80km) in coastal lowland woodland below the 90m contour. Its restricted distribution is determined by very high seasonal rainfall, a mean dry quarter precipitation usually greater than 100mm and a woodland blend of vegetation that is shaped and maintained by fire. The presence of one of the northern bloodwoods (*Eucalyptus intermedia*, *E. clarksoniana* or *E. dolichocarpa*) and an accompanying species of 'bird-syndrome' arillate *Acacia* are suggested as a minimal basis for suitable habitat. Among exudivores, *Petaurus gracilis* appears to be more a dietary opportunist, feeding on nectar, pollen, arthropods, *Acacia* exudates, lerp, and honeydew when these items become seasonally available. More notable dietary items include *Acacia* arils, *Xanthorrhoea* scape exudates and sap (or kino) of *E. intermedia*. Interpretation of its socioecology was impeded by small sample size but home range size for an adult female was determined at 23ha and a quasi-polygynous mating system was suggested. *Petaurus gracilis* is endangered throughout its range by habitat destruction, fragmentation and changes in local fire regimes that together have resulted in an 80% loss of its preferred habitat. □ *Petaurus gracilis*, *Petaurus norfolcensis*, Petauridae, taxonomy, distribution, conservation, Queensland, Australia, Mahogany Glider, habitat, ecology, tropical woodland, diet, behaviour.

Steve Van Dyck, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 21 February, 1993

Since its description in 1883 by Charles de Vis, the taxonomic status and distribution of *Petaurus gracilis* has been a matter for conjecture. De Vis failed to designate a holotype and no specimens are referred to in the literature or known from collections outside the Queensland Museum. Five years after its description, Thomas (1888) synonymized *P. gracilis* with *P. norfolcensis* (then *Petaurus sciureus*) and Mackay (1988) dealt with it similarly. Other references to the name *P. gracilis* deal with it as a northern subspecies of *P. norfolcensis* (Iredale & Troughton, 1934; Troughton, 1941; Tate, 1945; Fleay, 1947; 1954; Marlow, 1962; Suckling, 1983; Alexander, 1981; Colgan & Flannery, 1992). Given the lack of *P. gracilis* specimens in collections, and the subsequent anonymity of the species, it is probable that its synonymy has resulted from a broad interpretation of de Vis's brief description rather than from a physical examination of the few *P. gracilis* specimens. Also, the assigning of *P. norfolcensis gracilis* to a wide range of Queensland examples of *P. norfolcensis* has resulted from too broad an interpretation of de Vis's loose reference

to its collection locality, 'North of Cardwell' (de Vis, 1883: 620).

In 1990 I reported three previously unregistered museum specimens, whose large size, long, thin, short-haired tails, pattern of fur colouration and measurements agreed closely with de Vis's description of *P. gracilis* (Van Dyck, 1990). These skins had been collected by Kendall Broadbent in 1886, from somewhere on, or near Mt Echo, 18km SW Cardwell. At the time of that report, given the faded, deteriorated quality of the skins, the fragmentary nature of cranial and dental material extracted from them, and inexplicable inconsistencies between the de Vis description and data associated with old identification tags attached to the skins, it was concluded that until additional material came to hand, *P. gracilis* should remain a junior synonym of *P. norfolcensis*. However, I also concluded that it was inappropriate to continue the use of *P. norfolcensis gracilis* in respect of all northeastern and mideastern Queensland examples of *P. norfolcensis* as they were indistinguishable from their more southern conspecifics.

In December 1989, living representatives of *P.*

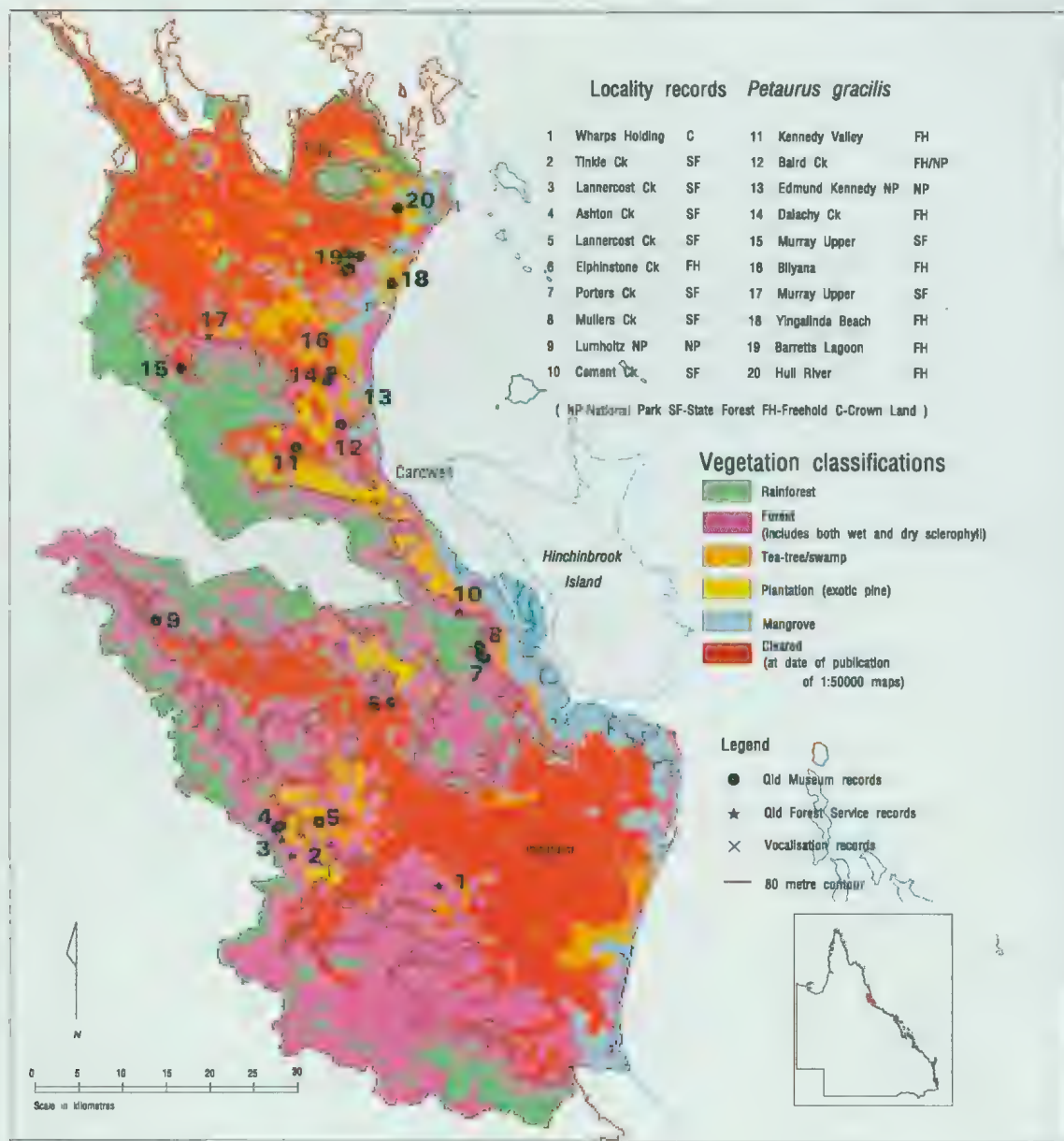


FIG. 1. Locality records for *Petaurus gracilis* (see Table 1 for details).

gracilis were located on freehold land at Barretts Lagoon (18°02'S, 145° 58'E), 14km SE of Tully. At that time, one specimen (JM7605) was collected for museum accession. In January 1990 the collection site was cleared for cultivation of bananas and pineapples. In February 1991 an adult female was captured nearby, photographed (Fig. 2) and subsequently (May) released at the site of

capture (Van Dyck, 1992a). Further surveys conducted during 1991-2 extended and refined the range of the species and provided data suggesting that the long-term conservation of the species could be a matter of grave concern.

The aim of the present study was to: 1, clarify the taxonomic status of *P. gracilis* with respect to *P. norfolcensis* (in particular) and other members

of the genus; 2, provide preliminary data on the distribution, habitat requirements, diet and socioecology of *P. gracilis*; and 3, assess the conservation status of the species.

METHODS

SYSTEMATICS

Nomenclature for molar tooth structure follows Woodburn et al. (1987), and cheek tooth number follows Archer (1978) (see explanation in Marshall, 1987). Dental and cranial measurements were made after the method shown in Fig. 3. Specimens were measured to the nearest 0.01mm using NSK electronic digital calipers. Specimens compared in diagnoses were adults with fully erupted fifth molars. T-tests were used to test for statistical significance.

Specimens from the following institutions were examined: Queensland Museum (specimens referred to in text prefixed by J or JM); Australian Museum, Sydney (specimens prefixed by M); Australian National Wildlife Collection, Division of Wildlife Research, Canberra; Bishop Museum, Honolulu; British Museum (Natural History),

London; American Museum of Natural History, New York; Museum of Victoria, Melbourne. Maximum numbers of individuals included in statistical analyses were: *P. norfolcensis* 70, *P. breviceps* 21, *P. australis* 11, *P. abidi* 5 and *P. gracilis* 11. Old skins (JM5521, JM5522, JM5523) were omitted from statistical analyses.

FIELD SURVEYS

Field observations and surveys were made during the following periods: 1-13 Dec 1989, 9-24 Feb 1991, 9-24 May 1991, 2-16 Aug 1991, 23-29 Nov 1991, 29 Feb-13 Mar 1992, 13-14 May 1992, 24 May-6 June 1992, 26 Sept-11 Oct 1992, 24-26 Nov 1992. Fieldwork during 1989 and 1991 concentrated on capture and radiotelemetry of individuals at Barretts Lagoon, while 1992 fieldwork was concerned with an assessment of distribution outside the immediate area of the lagoon.

CAPTURE TECHNIQUES

Wire cage and aluminium live traps were set 2-7m above the ground. Traps included Elliott aluminium (460×160×150mm and 330×95×100mm) Mascot wire (560×205×215mm),

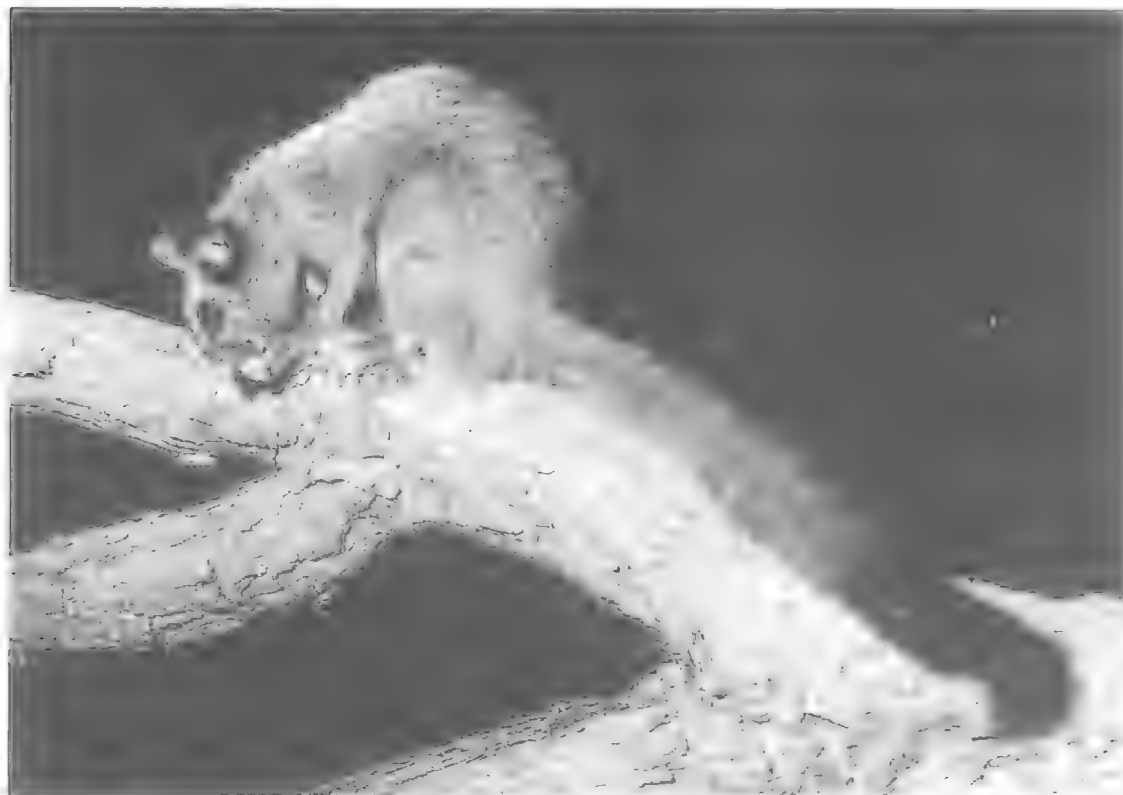


FIG. 2. Adult female *Petaurus gracilis* T4026, caught Barretts Lagoon 22 Feb 1991, released 11 May 1991

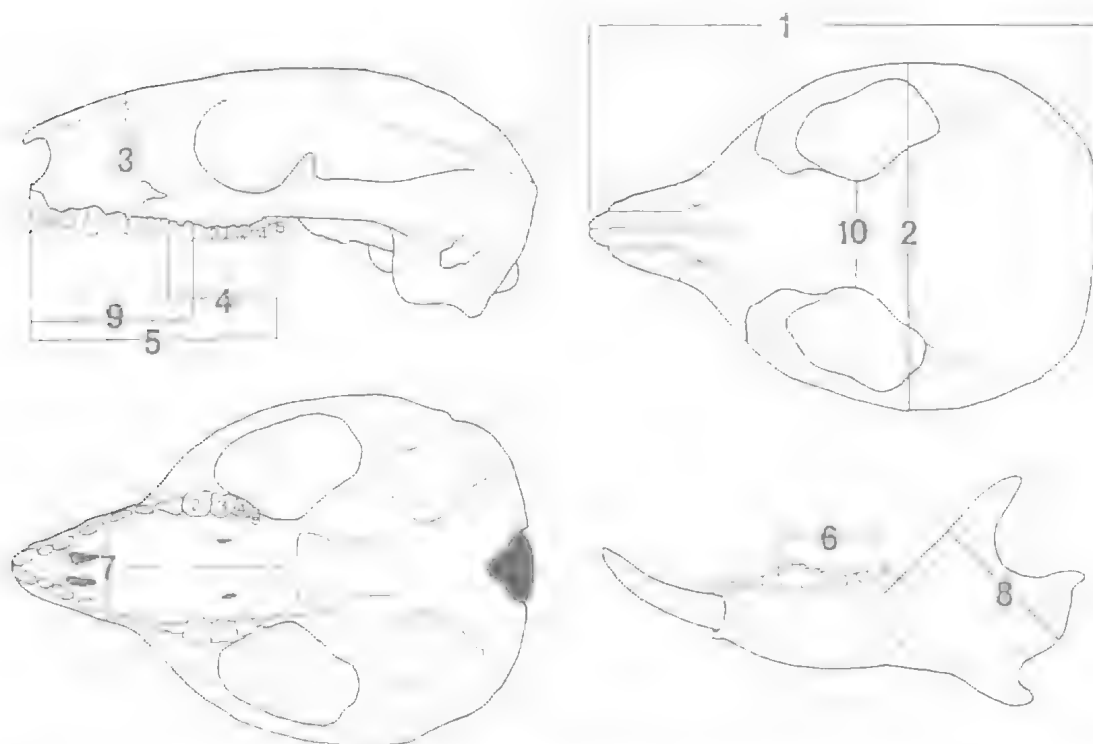


FIG. 3. Method used in skull and tooth measurement. 1, maximum skull length; 2, zygomatic width; 3, rostrum height; 4, upper molar row length; 5, upper tooth row length; 6, lower molar row length; 7, rostral width between upper canines; 8, width of ascending ramus; 9, upper incisor-premolar row; 10, interorbital width.

Tamohawk wire ($400 \times 140 \times 140$ mm) and Acme wire ($440 \times 200 \times 180$ mm). Traps were protected by plastic bag weather shields and supported on horizontal ply baseboards screwed to right-angle iron brackets which were nailed to tree trunks. Baits consisted of a sugar/honey toffee or a mixture of honey and sweetened condensed milk. Additional attractants of diluted honey, sugar water or raspberry cordial were sprayed on tree trunks near trap entrances to lure gliders into the traps. Traps were laid along transects on trunks of living and dead trees, or arranged in groups of up to 12 among flowering *Xanthorrhoea johnsonii* chosen for signs of *P. gracilis* visitation by way of footprinted flower stalks. Trapping was carried out during the following periods: 1-13 Dec 1989 (205 trap nights); 9-24 Feb 1991 (230 trap nights); 9-24 May 1991 (110 trap nights); 29 Feb-13 Mar 1992 (176 trap nights). Trap-nights totalled 721 and covered 10 sites at Barretts Lagoon and one at Edmund Kennedy National Park, Cardwell.

At the beginning of the survey (Feb and May

1991), 48 artificial nesting hollows were installed and left for between 16-19 months at 2 sites at Barretts Lagoon to act as a back-up should the trapping program fail. Of these, 34 were attached to tree trunks (Feb 21) at the Barretts Lagoon 'Rice Fields' ($18^{\circ}01'S$, $145^{\circ}58'E$) where an adult female had been caught (19 Feb). This 200-400m wide strip of woodland was bordered to the west by Barretts Lagoon Road and to the east by natural treeless swales (Fig. 19). Given the irregular shape of the site, the 34 hollows were arranged in a grid of six rows (1 row of 7 hollows, 2 of 6, 3 of 5) with minimum spacings of approximately 50m. On 17 May 1991, 14 additional artificial nests were installed further east ($18^{\circ}01'S$, $145^{\circ}59'E$) and set along 700m of north-south track and spaced at 50m. The choice of 'nest' design was based roughly on the trap of Mawbey, (1989) which was shown to be highly effective for catching sugar gliders *P. breviceps* in the field. The artificial nesting hollows used in my study were of 160mm (diameter) PVC sewer pipe cut to 500mm lengths, capped at either end and



FIG. 4. One of 48 PVC artificial nest hollows used in the survey. Each was strapped onto a trunk with fencing wire.

drilled with a 65mm (diameter) entrance hole 120mm from the top of the tube (tube vertical). These hollows were furnished internally with a 280mm 'ladder' of roughened timber screwed directly below the entrance hole while the floor was perforated for drainage. All tubes were painted a dull brown-green, numbered and strapped vertically to trunks at heights of 3-7m using fencing wire (Fig. 4). All tubes were inspected at least once per survey period and all but one (occupied by a family of *P. breviceps*) were removed from the two sites by 8 Sept 1992.

One *P. gracilis* (Fig. 2) was captured in a mist-net enclosure constructed around the outside of its den in a hollow Swamp Mahogany trunk (see Van Dyck, 1992a). Two were captured by 'port-holing' hollow trunks of known nest trees. This practice involved cutting a rectangular hole (approx 120mm \times 180mm) into the den and extracting the glider(s) by hand. The 'port-hole' was then plugged with a hardwood block which was

wired for later access. One individual was caught by shaking it from a small tree (see Van Dyck, 1992b).

HANDLING AND RADIO-TRACKING PROCEDURES

Captured individuals were weighed, measured, sexed, assigned to an age category from the condition of wear of the first upper incisors (Suckling, 1980; Alexander, 1981), tagged on one ear with a numbered (T40_ _) fingerling ear-tag ('FF', Salt Lake Stamp Co., Utah) and (where possible) released back into the den from which they were taken. Gliders used in radio tracking were fitted with a Titley (Ballina, NSW) 'Micro-lite', two-stage transmitter either attached to a soft leather collar with a protruding 15cm whip antenna or epoxy-potted into a small disc (diameter 26mm \times 10mm high) with a protruding 28cm antenna. The ventral surface of the epoxy disc transmitter was glued to the animals mid-back (Selleys Supa Glue) after a circle of fur approximating the diameter of the disc had been cropped close to the glider's skin. The short hair stubble that remained, provided a rough bonding surface for the glue on the transmitter and at the same time protected the animal's skin from contact with the adhesive. Long hair surrounding the positioned disc was then glued over the dorsal surface of the transmitter, in effect hiding it and leaving only the whip antenna exposed. The total weight of the transmitter package was approximately 11g. A 2000 channel 'Regal 2000' (Titley) portable receiver operating on the 150.000-151.999MHz band, and a 2 element hand-held H-frame antenna were used to locate animals.

HOME RANGE DETERMINATION

Preliminary home range estimates were determined for one adult female (T4026) and two sub-adult female gliders (T4027 and T4028, presumed to be the offspring of T4026). During the course of the study only one male (T4030) was captured and radio-tagged. This male dislodged its transmitter on the third day and only den site data was recorded. Although gliders were strictly nocturnal, a morning (0600hrs) and afternoon (1600hrs) den fix was usually taken for each tagged animal. Because animals proved difficult to catch and visits to the area were irregular (and often 3-4 months apart), animals were radio-tracked both continuously and randomly during each visit. Direct observation was used to maximise return of information other than that associated solely with home range. Trees visited on a

Site	Locality	Lat.	Long.	Alt.m asl.	Nature of record (No. recorded)	Dates	Collector/ Observer	Tenure
i	"North of Cardwell"	—	—	—	species description de Vis (1883)	1883	K. Broadbent	—
ii	"Mt Echo"	—	—	—	JM5521 (AM) JM5522 (AF) JM5523 (AF)	1886	K. Broadbent	—
1	*Wharps Holding	18°41'18"S	146°04'25"E	20-40	sighting (2)	13.10.92	L. Logan T. Eyre	Crown
2	*Tinkle Creek	18°39'20"S	145°54'55"E	40	sighting (1)	15.10.92	T. Eyre	S.F.
3	*Lannercost Creek	18°38'20"S	145°54'15"E	90	sighting (1)	15.10.92	T. Eyre	S.F.
4	Ashton Creek	18°37'41"S	145°53'57"E	70	sighting (1)	01.06.92	S. Van Dyck S. Burnett	S.F.
		18°37'26"S	145°54'12"E	60-70	sighting (2)	01.06.92	"	S.F.
5	Lannercost Creek	18°37'13"S	145°56'44"E	30-40	sighting (1)	01.06.92	"	S.F.
6	Elphinstone Creek	18°29'42"S	146°01'26"E	20-40	sighting (1)	11.03.92	"	Freehold
		18°26'57"S	146°07'35"E	35	JM9015 (AF)	10.03.92	"	S.F.
7	Porters Creek	18°26'47"S	146°07'17"E	35	sighting (1)	13.05.92	S. Van Dyck J. Kehl I. Rob	S.F.
8	Mullers Creek	18°26'13"S	146°07'15"E	20-40	sighting (2)	13.05.92	"	S.F.
9	Lumholtz N.P.	18°24'30"S	145°46'10"E	40-60	sighting (1)	11.03.92	S. Van Dyck S. Burnett	N.P.
10	*Cement Creek	18°23'55"S	146°05'57"E	20-40	sighting (1)	12.10.92	C. Corben	S. F.
11	Kennedy Valley	18°13'31"S	145°55'23"E	0-20	JM8549 (AF)	-10.90	E. Gallipo	Freehold
				0-20	JM8550 (joey F)	-10.90	"	Freehold
12	Baird Creek	18°12'11"S	145°58'17"E	0-10	sighting (1)	05.03.92	S. Van Dyck S. Burnett	Freehold/ N.P. border
13	Edmund Kennedy N.P.	18°12'04"S	145°59'14"E	0-20	call (1)	05.03.92	"	N.P.
		*18°08'43"S	145°57'50"E	0-20	call (1)	04.03.92	"	N.P.
14	Dalachy Creek	18°09'26"S	145°57'26"E	0-10	JM9014 (AM)	08.03.92	"	Freehold
		18°08'51"S	145°57'40"E	0-10	sighting (2)	03.03.92	"	Freehold
15	Murray Upper	18°08'38"S	145°47'54"E	40-60	JM9016 (AF)	10.03.92	"	S.F.
16	Bilyana	18°07'S	145°56'E	0-20	private mount	-10.74	T. Marsilio	Freehold
17	*Murray Upper	18°06'30"S	145°49'40"E	20-40	sighting (1)	16.10.92	C. Corben	S.F.
18	Yingalinda Beach	18°03'18"S	146°01'37"E	0-10	sighting (1)	18.08.91	S. Van Dyck P. Stumkat	Freehold
	Barretts Lagoon i. South- west bank	18°02'31"S	145°58'36"E	0-10	JM7400 (AM)	09.12.89	"	Freehold
				0-10	sighting (8)	06.12.89- 08.12.89	"	Freehold
19	Barretts Lagoon ii. North- east bank	18°02'23"S	145°58'46"E	0-10	sight(1) & call (1)	09.08.91	P. Stumkat	Freehold
		18°02'22"S	148°58'52"E	0-10	JM7290 (AF with joey's JM9729 & JM9730)	14.02.73	G. Gordon R.J. Grimes	Freehold
	Barretts Lagoon iii. "Rice Fields	18°01'26"S	148°58'46"E	0-10	sighting (10)	15.02.91- 02.03.92	S. Van Dyck P. Stumkat S. Burnett B.&C. Cowell	Freehold
	Barretts Lagoon iv East	18°01'33"S	145°59'34"E	0-10	sight (9) & call (2)	17.05.91- 29.11.91	"	Freehold
20	Hull River	17°58'29"S	146°02'02"E	0-20	sighting (1)	2.10.92	S. Van Dyck S. Burnett	Freehold

glider's traversed route were marked with flagging tape and surveyed during the day.

It is acknowledged that direct observation through continuous tracking may have led to an underestimation of home range size through loss of independence of fixes (Swihart & Slade, 1985). To overcome this problem, where continuous tracking was employed, 30 minute fixes were extracted from examination of each route plotted through time. Quin et al. (1992) considered that 30min radio fixes for fast moving mammals such as species of *Petaurus* were adequate to assume independence of data points. Fixes were taken from adult female T4026 over a period of 4 full nights and 13 partial nights (including den fixes) during May, August and November 1991 (110 fixes), while those from sub-adult female T4028 were taken over a period of 1 full night and 9 partial nights (including den fixes) during May 1991 (36). Fixes from sub-adult female T4027 were taken over a period of 1 full night and 6 partial nights (including den fixes) during May 1991 (36 fixes). Estimates of home range area were generated using the harmonic mean distance minimum (HM) using 95% isopleths (see Dixon & Chapman, 1980) and the minimum convex polygon (MCP; Mohr 1974). The utility and appropriateness of the HM for describing home ranges of animals such as sugar gliders was demonstrated by Quin et al. (1992). Estimates were generated with the RANGES IVm software package (R. E. Kenward; Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, United Kingdom).

SPOTLIGHTING

12 volt, 150mm and 230mm 'Powa Beam Spotlights' (Byron Bay, NSW) were used from a vehicle, the 230mm (9") 'Powa-lite' (1 million CP, quartz halogen) being particularly efficient. 150mm, 12V spotlights powered by wet cell motorbike batteries were used for on-foot surveys. 3 and 4 'D'cell 'Mag-Lite' torches (Mag Instruments - Ontario, Calif) were used to observe radio-tagged animals. The expanding beam of these torches greatly facilitated detection of gliders leaping from treetops. A total of 1334 man-hours were spent spotlighting for *P. gracilis* (Table 3). *Petaurus gracilis* was consistently difficult to locate (see Davey, 1984; Menkhorst et al., 1988 for similar problems with *P. norfolcensis*). It was practically silent, evasive in spotlights

and its eyes reflected poorly (dull red). Animals attracted by playback recordings of *P. norfolcensis* or *P. gracilis* vocalisations (see Kavanagh & Rohan-Jones, 1982) or by imitated calls aborted their approach if a light was turned on. In approximately 877 manhours of non-telemetry spotlighting (547 hours from a vehicle, 330 on foot), 22 of the 28 animals located by this method were first observed from a vehicle.

PALYNOLOGICAL ANALYSIS

Pollen analysis was undertaken by M. Dettmann (University of Qld) on five faecal samples collected between Feb and Nov 1991 from Barretts Lagoon. Two strew slides were prepared from each sample. One, contained crushed but otherwise untreated faecal material mounted in glycerine jelly under a glass coverslip. The second slide contained faecal material treated with warm 5% KOH for 5min, then washed thoroughly under distilled water and sieved through a 240µ mesh screen prior to mounting in glycerine jelly. The untreated slides were examined to estimate relative proportions of pollen, other plant tissue and insect fragments in each sample, and to estimate the proportion of pollen with their contents (intine) in place. Qualitative and quantitative analyses of the pollen assemblages represented in each sample were determined from the treated slide.

VEGETATION ANALYSES

At each site where a glider had been observed (Table 1) the vegetation was assessed visually and classified into one of the vegetation types of Tracey (1982). A vegetation proforma was prepared by W. Lavack and R. Cummings (Queensland Department of Environment and Heritage) for each site. Trees, shrubs and grasses were recorded in terms of their relative abundance (A-abundant, C-common, O-occasional, U-uncommon). An estimate was made of projective foliage cover (% of the sample site occupied by the vertical projection of foliage only, see McDonald et al., 1984) and the soil type noted. Nest sites of four individuals were described in more detail by P. Stunkat and I after the manner of Menkhorst et al. (1988). A square quadrat, centered on a frequently used denning tree, was defined with its apices 30m to the N, S, E, and W (total area 1800m²). Densities of trees were then presented as mean number of trees per 1000m². Within each quadrat all trees and shrubs

TABLE 1. Site and record details for *P. gracilis* sorted from the south by 'triangle'. Age as adult (A) or juvenile (J). Sex as male (M) or female (F). Tenore includes National Park (N.P.)³ and State Forest (S.F.) *Site inside (east of) NP fence, but fence west of gazetted park boundary. + Record courtesy of J. Keld, QFS.

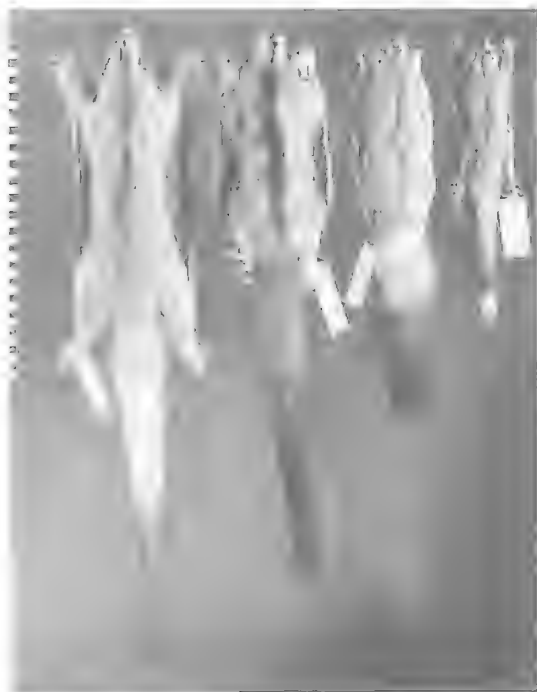


FIG. 5. Comparison of size in four species of *Petaurus*. L to R, *P. gracilis* (adult male JM9014, Dalachy Creek), *P. abidi* (adult female M21664, Wilbeite, Papua New Guinea), *P. norfolcensis* (adult female J11514 Warwick), *P. breviceps* (adult female JM7396, Barretts Lagoon). Scale divisions in cm.

taller than 3m were identified, counted and their height and circumference-at-breast-height measured (Table 4).

BIOCHEMICAL ANALYSIS

Frozen tissues of adult female JM8459 (Kennedy Valley) were the subject of electrophoretic allozymic analysis as described by Colgan & Flannery (1992).

SYSTEMATICS

Petaurus gracilis (de Vis, 1883)

DIAGNOSIS

Petaurus gracilis is distinguished from *P. norfolcensis* by its larger size, reflected in the following measurements (in mm) for which respective values show no overlap:

Maximum skull length: mean 51.14, R= 49.80-52.60, N= 7, SD= 0.95 vs 45.33, R= 40.96-49.05, N= 68, SD= 1.80.

Zygomatic width: mean 34.14, R= 32.90-35.08, N= 7, SD= 0.71 vs 30.15, R= 27.81-32.59, SD= 1.19.

Rostrum height: mean 14.02, R= 13.00-15.93, N= 9, SD= 0.84 vs 11.54, R= 9.89-12.68, SD= 0.62.

Tail-vent length: mean 353.50, R= 300-390, N= 10, SD= 25.76 vs 239.43, R= 195-290, N= 30, SD= 22.06.

P. gracilis has a significantly ($P < 0.001$) narrower interorbital width than *P. norfolcensis*: mean 8.59, R= 7.30-9.82, N= 9, SD= 0.95 vs 9.60, R= 7.97-11.73, N= 69, SD= 0.70.

P. gracilis is significantly ($P < 0.001$) larger than *P. norfolcensis* in the following measures (Fig. 5):

Head-body length: mean 247.45, R= 215-265, N= 11, SD= 15.86 vs 200.72, R= 165-232, N= 29, SD= 17.17.

Hind foot length: mean 39.61, R= 37-43, N= 11, SD= 2.00 vs 32.03, R= 24-38, N= 29, SD= 3.01.

Weight: mean 349.45, R= 255-410, N= 11, SD= 39.69 vs 170.47, R= 110-301, N= 30, SD= 43.57.

Upper molar row length: mean 8.68, R= 8.30-9.00, N= 9, SD= 0.21 vs 8.06, R= 7.37-8.90, N= 70, SD= 0.34.

Upper tooth row length: mean 23.90, R= 23.00-24.80, N= 9, SD= 0.51 vs 21.78, R= 19.76-23.51, N= 69, SD= 0.84.

Lower molar row length: mean 9.43, R= 9.00-9.91, N= 9, SD= 0.28 vs 8.73, R= 7.73-9.50, N= 69, SD= 0.34.

Upper incisor-premolar row length: mean 16.03, R= 15.47-16.59, N= 9, SD= 0.34 vs 14.46, R= 12.95-15.99, N= 69, SD= 0.69.

Rostral width between upper canines: mean 9.69, R= 9.10-10.30, N= 9, SD= 0.29 vs 8.67, R= 7.60-10.00, N= 69, SD= 0.46.

Width of ascending ramus: mean 13.13, R= 12.09-13.70, N= 9, SD= 0.32 vs 11.15, R= 9.93-12.50, N= 69, SD= 0.59.

Figs 6, 7 and 8 demonstrate the relationship between *P. gracilis* and *P. norfolcensis* for some of the measures referred to above.

Petaurus gracilis is distinguished from *P. breviceps* by its much larger size, reflected in the following measurements for which respective values show no overlap:

Maximum skull length: mean 51.14 vs 36.07, R= 33.17-37.91, N= 17, SD= 1.23.

Zygomatic width: mean 34.14 vs 24.79, R= 22.53-26.53, N= 16, SD= 1.20.

Rostrum height: mean 14.02 vs 8.92, R= 8.29-9.55, N= 19, SD= 0.36.

Width of ascending ramus: mean 13.13 vs 8.18, R= 7.28-9.49, N= 20, SD= 0.56.

Tail-vent length: mean 353.50 vs 192.92, R= 159-235, N= 13, SD= 19.62.

Weight: mean 349.45 vs 93.09, R= 59-118, N= 11, SD= 19.19.

Upper molar row length: mean 8.68 vs 6.37, R= 6.05-7.75, N= 21, SD= 0.20.

TABLE 2. Queensland Museum specimens (prefixed JM) and tagged individuals caught and released (prefixed T). Age as adult (A), sub-adult (SA) or juvenile (J). Sex as male (M) or female (F). Measurements in mm, weight in g. Tail damaged as (d).

Regn #	Locality	Age	Sex	HB	TV	HF	E	Wt	Preservation	Colour phase & comments
JM5521	Mt Echo	A	M	260	365	38	25	—	skin, skull	measurements from old buff skins
JM5522	Mt Echo	A	M	255	340	33	25	—	skin, skull frag	
JM5523	Mt Echo	A	F	252	355	37	25	—	skin, skull frag	
JM7290	Barretts Lagoon	A	F	261	330	42	35	352	skin, skull spirit	buff
JM9729	Barretts Lagoon	J	F	58	60	12	8	—	spirit	hairless young of JM7290
JM9730	Barretts Lagoon	J	F	48	59	11	8	—	spirit	hairless young of JM7290
JM7400	Barretts Lagoon	A	M	265	335	43	36	410	skin, skull, spirit	buff
JM8549	Kennedy Valley	A	F	240	270(d)	38	33	350	spirit	buff
JM8550	Kennedy Valley	J	F	95	121	20	15	43	spirit	buff, pouch young of JM8549
JM9014	Dalachy Ck	A	M	249	354	41	35	350	skin, skull, frozen body	dark
JM9015	Porters Ck	A	F	264	360	40	32	407	skin, skull, frozen body	
JM9016	Murray Upper	A	F	256	346	41	33	370	skin, skull, frozen body	'aberrant' phase
T4026	Barretts Lagoon	A	F	220	300	37	29	345		dark, caught in den 22.02.91
T4027	Barretts Lagoon	SA	F	200	320	32	31	195		dark, caught in nest box #8 10.05.91
T4028	Barretts Lagoon	SA	F	180	330	35	-	215		dark, caught in nest box #8 10.05.91
T4029	Barretts Lagoon	A	F	250	390	38	27	255		buff, caught while feeding 19.05.91
T4030	Barretts Lagoon	A	M	247	380	38	29	350		buff, caught in den 05.06.91
T4031	Barretts Lagoon	A	F	215	380	37	34	375		buff, caught in den 03.08.91
T4032	Barretts Lagoon	J	M	120	165	20	17	65		buff, nestling of T4026 26.11.91
T4033	Barretts Lagoon	J	F	120	175	24	17	69		buff, nestling of T4026 26.11.91

Upper tooth row length: mean 23.90 vs 16.90, $R=16.04$ -17.93, $N=20$, $SD=0.54$.

Lower molar row length: mean 9.43 vs 6.99, $R=6.60$ -7.91, $N=21$, $SD=0.28$.

Upper incisor-premolar row length: mean 16.03 vs 11.05, $R=10.24$ -12.14, $N=20$, $SD=0.48$.

Rostral width between upper canines: mean 9.69 vs 6.79, $R=6.29$ -7.30, $N=20$, $SD=0.31$.

Petaurus gracilis is immediately distinguished from *P. abidi* by the atrophied condition of P^2 in *gracilis*, but which, in *abidi*, is well developed and subequal in crown height to both P^1 and P^3 . *P. gracilis* is further distinguished by its reduction in buccal ectoloph enamel on M^2 and M^3 and by the reduction in the paracone relative to the metaconule (the posterolingual cusp previously and commonly termed the hypocone; see Woodburn et al., 1987: 641 for discussion) in M^2 . *P. gracilis* is also distinguished from *P. abidi* by its smaller dimensions in the following measure-

ments for which respective values show no overlap:

Interorbital width: mean 8.59 vs 10.42, $R=9.70$ -11.50, $N=3$, $SD=0.78$.

Upper molar row length: mean 8.68 vs 9.50, $R=9.30$ -9.70, $N=2$, $SD=0.21$.

Petaurus gracilis is distinguished from *P. australis* by its smaller size, reflected in the following measurements (for which respective values show no overlap:

Zygomatic width: mean 34.14 vs 37.38, $R=34.98$ -39.70, $N=10$, $SD=1.45$.

Tail-vent length: mean 353.50 vs 433, $R=410$ -460, $N=6$, $SD=17.88$.

Interorbital width: mean 8.59 vs 11.51, $R=10.65$ -12.22, $N=11$, $SD=0.38$.

Rostral width between upper canines: mean 9.69 vs 12.00, $R=11.06$ -12.70, $N=11$, $SD=0.53$.

Ear length: mean 31.96, $R=27$ -36, $N=10$, $SD=2.85$ vs 51.40, $R=46$ -56, $N=5$, $SD=3.88$.

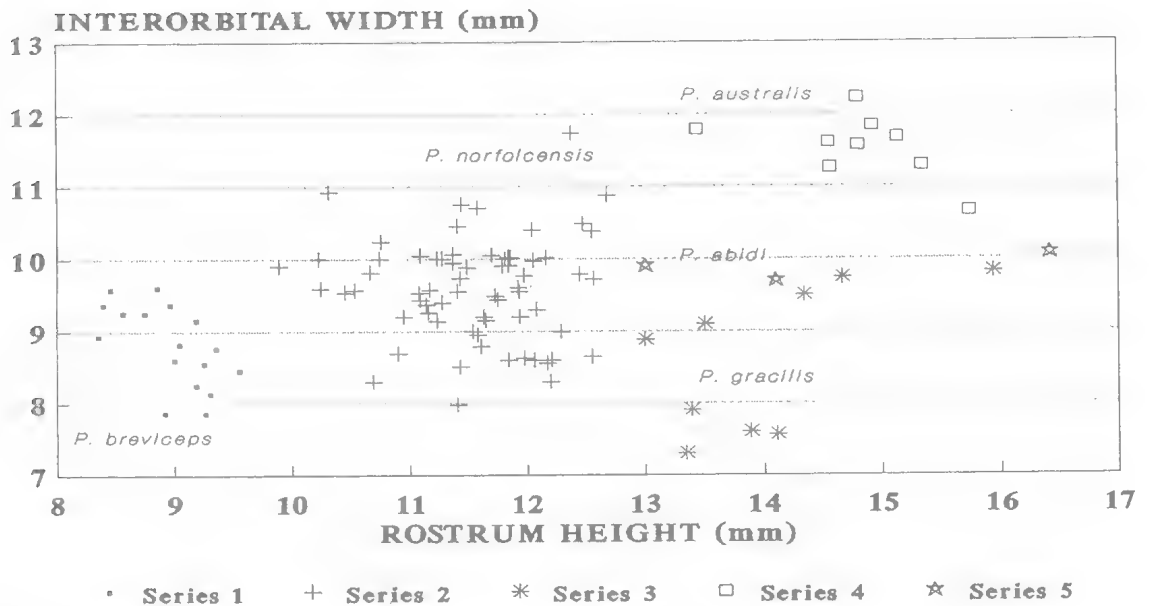
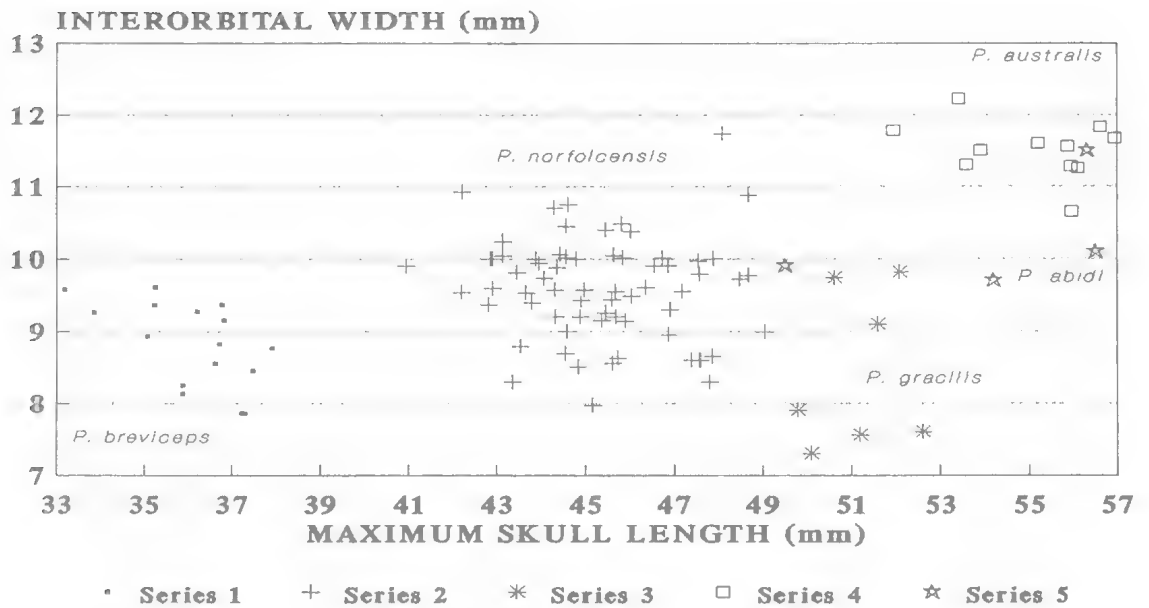


FIG. 6. Bivariate plots of interorbital width against rostrum height and maximum skull length. Series 1= *P. breviceps*, Series 2= *P. norfolcensis*, Series 3= *P. gracilis*, Series 4= *P. australis*, Series 5= *P. abidi*.

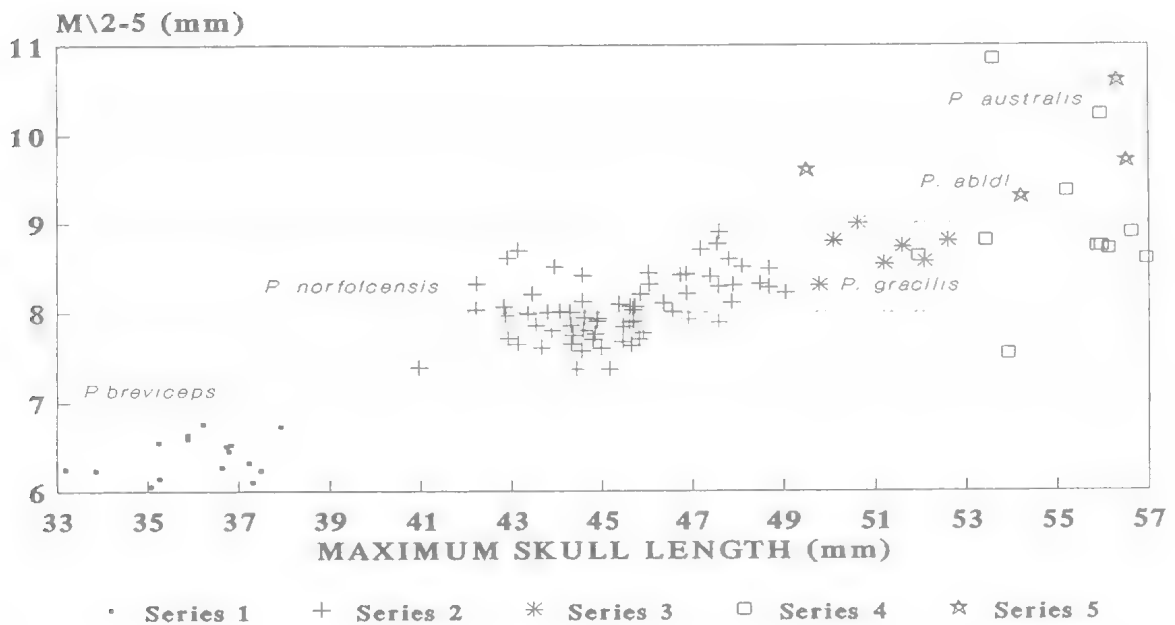
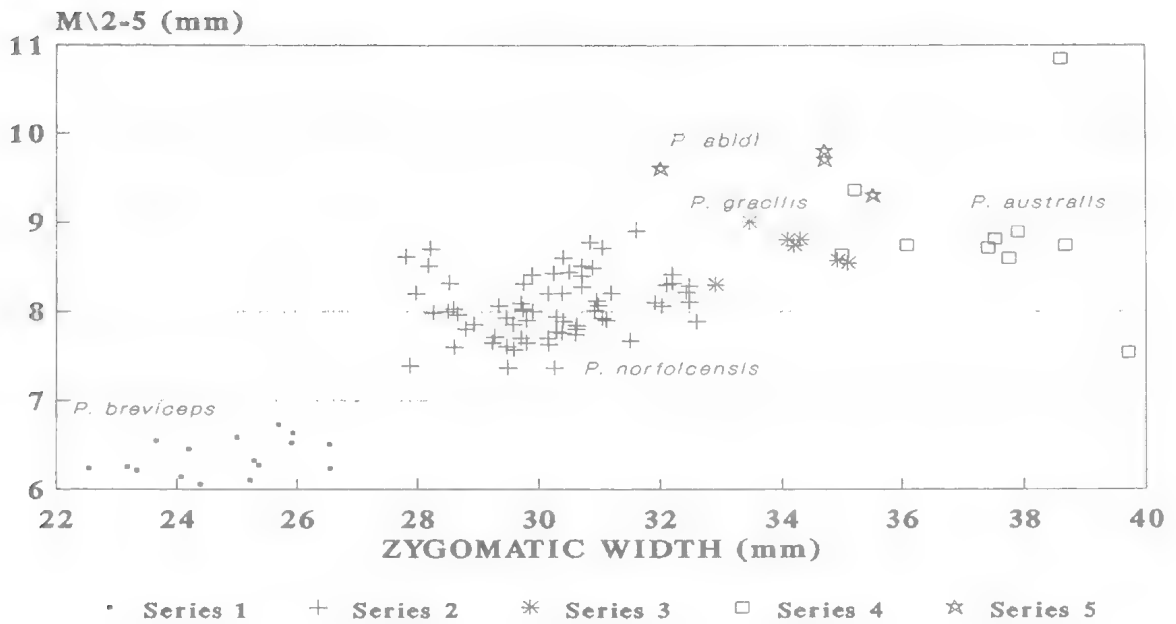


FIG. 7. Bivariate plots of upper molar row (M2-5) against zygomatic width and maximum skull length. Series 1 = *P. breviceps*, Series 2 = *P. norfolcensis*, Series 3 = *P. gracilis*, Series 4 = *P. australis*, Series 5 = *P. abidi*.

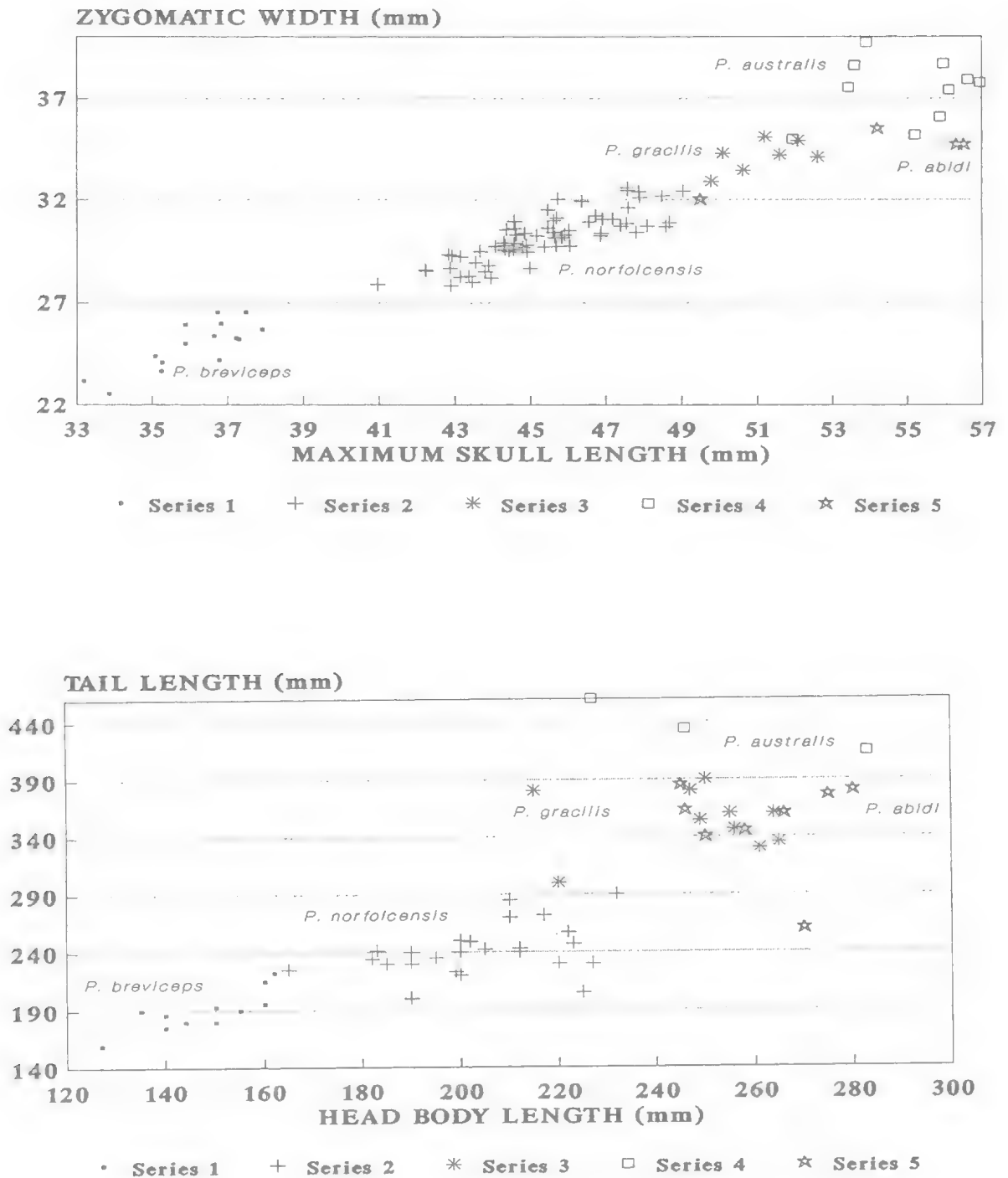


FIG. 8. Bivariate plots of zygomatic width against maximum skull length, and head body length against tail length. Series 1= *P. breviceps*, Series 2= *P. norfolcensis*, Series 3= *P. gracilis*, Series 4= *P. australis*, Series 5= *P. abidi*.

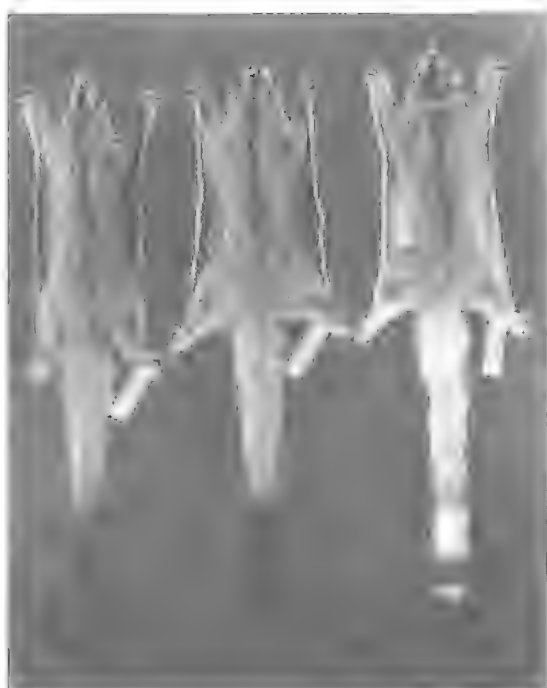


FIG. 9. Dorsal perspective of three colour morphs in *P. gracilis*. L to R, dark phase (adult male JM9014), buff phase (adult female JM9015), aberrant phase (adult female JM9016).

DESCRIPTION

Externally, this species of *Petaurus* is distinctive for its large size, long, relatively short-haired tail and buff to mahogany-brown belly (Figs 5, 9, 10). There is considerable variation in the depth of both dorsal and ventral tonings and the band of fur along the lateral anterior edge of the gliding membrane may be buff, rich orange or deep mahogany. Ventral fur (adult and sub-adult of both sexes) may be either buff, honey-yellow or deep mahogany (Figs 9, 10; Table 2).

Pelage: Colours (where capitalised after Ridgway, 1912) of the buff phase (example used JM7400) are as follows: Fuscous-Black mid-dorsal head-and-body stripe variable in width (partially depending on the 'lie' of the body fur) commencing at a point between the anterior edge of the eyes and extending posteriorly to the rump. It is 12mm wide between the ears, 5.6mm at mid-neck, 17mm at mid-shoulder blades and fading away over the rump. Fur of the mid-back (16.3mm long) with basal 14.4mm Smoke Gray, median 1.4mm either Pale Smoke Gray (off-white) or Chamois (brown-yellow), apical 0.5mm Fuscous-Black. The back therefore appears overall a patchy wash of smoky grey

(Smoke Gray) and yellowish-brown. The yellowish patches are most pronounced over the shoulders, along the flanks and over the rump. Medially thickened Fuscous-Black-tipped guard hairs are interspersed very sparsely through the fur and are 20.4mm on the mid-back and reduce to 3.6mm on the tip of the snout where they are entirely Fuscous-Black. Fur on either side of the head-stripe is Pale Smoke Gray with a yellowish-buff wash. A ring of Fuscous-Black fur encircles the eye, and fur below the eye-ring to the corner of the mouth is Pale Olive-Buff. Muzzle (delineated by the presence of mystacial vibrissae) a weak Fuscous-Black. Fuscous-Black fur encircles the dorsal posterior and ventral base of the pinna, extending forward and down to slightly posterior of the genal vibrissae. Directly anterior to the ear and posterior to the genal vibrissae, is a patch of anteriorly-directed Pale Olive-Buff fur. The pinna is virtually naked on the inner surface, and on the distal 11mm of the outer surface. The pinnae of living animals are a pink-bronze. A patch of pale Olive-Buff fur (hairs up to 8mm long) on the posterior external edge of the pinna forms a conspicuous tuft.

Dorsally, the patagium is fringed along its length by a thickly-turred band of Cream-Buff fur (hairs 3mm long). Midway between the wrist and digit 5, the apex of a triangular patch of striking Chamois-coloured fur extends in a narrowing band (to 5mm wide) posteriorly along the inner side of the outermost Cream-Buff band. More mesially, and slightly overlaying the Chamois band the patagium is coloured Sepia in a hard line 6mm wide and extending posteriorly from the wrist to the ankle. Sepia fur sparsely covers the rest of the patagium.

Ventrally, the patagium is fringed in a 5mm wide band of Clay coloured fur from the claw of digit 5 to the ankle. More mesially this band is partly overlaid by another 5mm wide band of Sepia which extends from 20mm posterior of the digit 5 claw to the ankle where its colour fades. The bulk of the patagium is then sparsely covered with 15mm long Honey-Yellow fur.

The soft ventral fur (18mm long on the belly) is Cream-Buff to Honey Yellow, but is suffused with Smoke Gray hairs on either side of the neck and around the muzzle.

Forefeet digits are thinly covered with Smoke Gray hairs. Hindfeet are more thickly covered with slightly lighter Pale Olive-Buff which contrasts with a 'mitten' of Smoke Gray over the metatarsals extending up to the inner posterior region of the thigh in a triangular stripe 23mm at

TABLE 3. Localities surveyed, spotlight effort and arboreal mammals recorded. Mammals are grouped by locality, not by date. Fruit bat presence not recorded.*Observed on dry *E. acmemoides* ridge. # Observed at approx. 610 m. a.s.l. ▲ Site cleared Feb 1990.

SURVEY AREA		Lat.	Long.	PERIOD	SPOTLIGHT MANHOURS	ARBOREAL SPP OBSERVED (N)
1. Bluewater		19°13-14'S	146°25-30'E	May 92	8	—
2. Rollingstone	Clemant S.F. west	19°05-06'S	146°25-27'E	May 92	13	<i>P.breviceps</i> (3+1 call)
				Jun 92	2	
	Clemant S.F. east	19°04-05'S	146° 25-27'E	May 92	16.5	<i>P.breviceps</i> (1) <i>T.vulpecula</i> (3)
				Jun 92	3	
				Sep 92	13.5	
3. Paluma turnoff		18°58' -59'S	146 °17-18'E	May 92	2	—
				Jun 92	7	
4. Amos Rd- coast- Crystal Ck		18°54-57'S	146°16-17'E	May 92	8	<i>T.vulpecula</i> (1)
5. Orient Ck		18°47-48'S	146°13-14'E	Sep 92	26	<i>T. vulpecula</i> (2)
6. Ashton Ck		18°37-38'S	145°53-56'E	Jun 92	18	<i>P. gracilis</i> (3) <i>T. vulpecula</i> (8)* <i>P. breviceps</i> (1)*
7. Lannercost Ck		18°37'S	145°56-58'E	Jun 92	6	<i>P. gracilis</i> (1)
8. Wallaman Rd		18°37'S	145°52-53'E	May 91	10	—
				Mar 92	1	
9. Manor Ck		18°29'S	146°03'E	Jun 92	15	<i>P. breviceps</i> (1)
10. Elphinstone Ck		18°29'S	146°01'E	Mar 92	4	<i>P. gracilis</i> (1)
11. Porters Ck		18°26'S	146°07'E	Mar 92	9	<i>P. gracilis</i> (2)
				May 92	9	
12. Mullers Ck		18°26'S	146°07'E	May 92	12	<i>P. gracilis</i> (2)
13. Yamanie N.P. Mt Echo		18°24-25'S	145°46-47'E	Jun 86	24	<i>P. gracilis</i> (1)
				Jul 88	18	
				Mar 92	6	
14. Henrietta Holding		18°24'S	145°45'E	Oct 92	11	—
15. Gowrie Ck		18°23-24'S	145°50'E	Jul 88	12	<i>P. volans</i> (1)
16. SE of 5 mile Ck		18°20-23'S	146°03-06'E	May 92	10	—
17. SW of 5 mile Ck		18°20-23'S	146°03-06'E	May 92	28	—
18. Macalister Mts		18°17-19'S	145°57-58'E	Jul 88	70.5	<i>D. lumholtzi</i> (1) <i>P. herbertensis</i> (4) <i>P. breviceps</i> (1)
19. Ellerbeck Rd		18°14'59"S	145°58'36"	Nov 92	2	<i>P. breviceps</i> (1)
20. Hinchinbrook Is		18°14'S	146°08'E	Sep 92	16	<i>U. caudimaculatus</i> (1)
21. Baird Ck		18°12'S	145°58'E	Mar 92	2	<i>P. gracilis</i> (1)
22. Kirrima-Blencoe Falls		18°09-14'S	145°32'-38'E	Mar 92	11	<i>T. vulpecula</i> (28) # <i>P. volans</i> (26) # <i>P. peregrinus</i> (11) # <i>P. breviceps</i> (2)# <i>A. pygmaeus</i> (1)#
23. Edmund Kennedy N.P.		18°08-11'S	145°58-59'E	Sep 91	31.5	<i>P. gracilis</i> (2 calls) <i>D. trivirgata</i>
				Mar 92	27	
24. Dalachy Ck		18°08-09'S	145°56-57'E	Mar 92	15.5	<i>P. gracilis</i> (3) <i>T. vulpecula</i> (2) <i>P.breviceps</i> (1)
25. Murray Upper		18°08'S	145°47'E	Mar 92	3	<i>P. gracilis</i> (1)
26. North Murray		18°05-06'S	145°46-48'E	Mar 92	11	—
27. Yingalinda Beach		18°03'S	145°59'E- 146°02'E	May 91	20	<i>P. gracilis</i> (1)
				Aug 91	24	
				Nov 91	16	

TABLE 3 cont. Localities surveyed, spotlight effort and arboreal mammals recorded.

SURVEY AREA	Lat.	Long.	PERIOD	SPOTLIGHT MANHOURS	ARBOREAL SPP OBSERVED (N)
28. Barretts Lagoon to Bedford Ck	18°02-04'S	145°58-59'E	Dec 89	30	<i>U. caudimaculata</i> (1) <i>D. trivirgata</i> (2) <i>P. brevicauda</i> (1)
			Feb 91	46	
			May 91	15.5	
			Sep 92	9	
29. ▲ Barretts Lagoon (southwest bank)	18° 02'S	145°58'E	Dec 89	115	<i>P. gracilis</i> (9) <i>P. brevicauda</i> (6) <i>D. trivirgata</i> (1) <i>A. pygmaeus</i> (2)
30. Barretts Lagoon (northeast bank)	18° 02'23"S	145°58'46"E	Sep 91	1	<i>P. gracilis</i> (1 + 1 call)
31. Barretts Lagoon ("Ricefields")	18°01'S	145°58'E	Feb 91	110	<i>P. gracilis</i> (10) <i>P. brevicauda</i> (4) <i>D. trivirgata</i> (1)
			May 92	68	
			Aug 91	249	
			Nov 91	18	
			Mar 92	5.5	
32. Barretts Lagoon (east)	18°01'S	145°59'E	May 91	10	<i>P. gracilis</i> (9 + 2 calls) <i>P. brevicauda</i> (3) <i>A. pygmaeus</i> (1)
			Aug 91	17	
			Nov 91	20	
			Mar 92	5.5	
			Sep 92	9	
33. Hall R	17°58'S	146°01-02'E	Oct 92	8	<i>P. gracilis</i> (1)
34. Mission Beach Rd	17°55-56'S	146°00-05'E	Oct 92	23	<i>D. trivirgata</i> (1)
35. Graham Ra N.P.	17°18-19'S	146°01'E	Oct 92	15	—
36. S of Daintree R, Mossman	16°17-18'S	145°25-26'E	Oct 92	12	—
			TOTAL	1334	

its widest point almost to the base of the tail. A similar, but darker forearm 'stripe' (Fuscous Black) extends from the base of digit 1 along the antero-mesial region of the forearm to terminate in a 20mm wide patch at the base of the forearm.

The tail is thinly haired and approximately one-and-a-half times longer (average 147%) than the head and body length. Near its base (40mm from the body) the fur is slightly shorter dorsally (25mm) and ventrally (17mm) than laterally (33mm). 40mm from the tip of the tail the fur is even in length and slightly shorter (24mm). The distal one-third of the tail is Fuscous Black changing reasonably abruptly to honey-grey (basal 20mm Smoke Gray, apical 13mm Chamois).

Males exhibit naked, ovoid glandular patches on the crown of the head within the black head-stripe (gland approx. 9mm × 5mm) and at the base of the throat (approx. 9mm × 7mm).

Vibrissae: Approximately 16 relatively short Fuscous Black mystacial vibrissae occur on each side and measure up to 19mm long; supra-orbital vibrissae (Fuscous Black) number approx. 2 each side, genals number 2-3 (Fuscous Black) and metatarsals number 4 (Chamois).

Claws of fore and hind feet are relatively large with maximum chord length of digit 4 and 5 claws approx 9mm. Digit 4 is the longest digit of manus or pes and digit 4>5>3>2>1.

In the dark phase (Figs 9, 10), white and buff colours are replaced with deep gingers, browns or Fuscous-Black. The pattern of body stripes, tail and limb 'pennants' is as in the buff form but the median section of mid-back varies from Tawny Olive to Deep Mouse Gray (not Pale Smoke-Gray), the head may be Tawny Olive to Pale Olive Gray, the cheeks and flanks Honey Yellow to Dark Olive-Gray (not Pale Olive-Buff), and the dorsal anterior flange of the patagium Honey Yellow to Deep Olive Yellow (not Chamois). The dorsal surface of the patagium is Deep Mouse Gray, its external margin Deep Olive-Gray, ventrally the patagium is fringed in a 5mm wide band of Deep Olive-Gray fur tipped with buff (the apical 1mm) from the claw of digit 5 to the ankle. More mesially this band is partly overlaid by another 5mm wide band of Fuscous-Black which extends from 20mm posterior of the digit 5 claw to the ankle where its colour fades. The bulk of the patagium is then sparsely covered with Deep

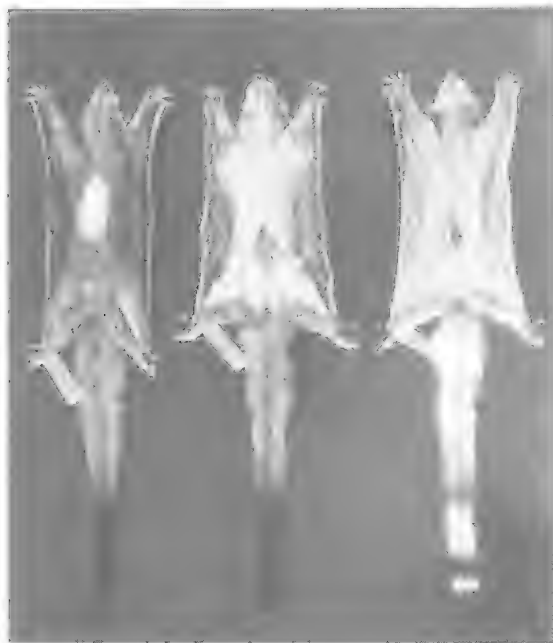


FIG. 10. Ventral perspective of three colour morphs in *P. gracilis*. L to R, dark phase (adult male JM9014), buff phase (adult female JM9015), aberrant phase (adult female JM9016).

Olive-Gray fur. Fur encircling the dorsal posterior and ventral base of the pinna, extending forward and down to slightly posterior of the genal vibrissae is Fuscous-Black. The ventral surface from throat to sternum is a Grayish Olive to Tawny Olive darkening to Sepia or Dark Olive near the belly. A small spot or streak of white fur may be present on the belly, sternum or slightly anterior to the pouch. The scrotum is buff-coloured, and hair inside the pouch Warm Sepia.

Aberrant form (Figs 9,10): JM9016 may represent an aberrant form where the ventral surface is more richly coloured with Clay Colour (orange-ochre) fur which extends around the forefeet up to the elbows, around the hind feet as far as the knees, and over the patagial edges to end along the animal's flanks. A small white patch of fur is present in the head-and-body stripe just posterior the ears. The tail is banded as follows (from the base), 11mm white, 14mm Mineral Gray, 50mm Tilleul Buff, 36mm Mineral Gray, 40mm Tilleul Buff, 57mm Mineral Gray, 26mm Fuscous (marking the proximal extent of a normal black tail-tip), 64mm Pale Olive-Buff, 40mm Fuscous-Black. Alexander (1981) illustrated an aberrant specimen, M8134, from Grafton, New South Wales similar to JM9016. He commented on the

possibility of M8134 being 'some sort of hybrid' between *P. breviceps* and *P. norfolcensis*. Given the size disparity between *P. breviceps* and *P. gracilis* and the observed intolerance of *P. gracilis* toward *P. breviceps* in the field, the likelihood of JM9016 representing a hybrid is probably remote.

Cranium and dentition: Essentially similar to *P. norfolcensis* except skull longer and much broader, with a much higher rostrum and wider ascending ramus. In spite of such consistently high values in *P. gracilis*, upper molar row lengths are not significantly longer than those of large examples of *P. norfolcensis*, and interorbital length in *P. gracilis* is significantly narrower than *P. norfolcensis* of all sizes (Figs 6-8).

Biochemical analysis: Electrophoretic allozymic analysis conducted by Colgan and Flannery (1992) showed *P. gracilis* to be genetically distinct (three fixed differences; adenylate kinase (1), glycerophosphate dehydrogenate and phosphoglucumutase in 21 loci) from *P. norfolcensis norfolcensis* (Limeburners Creek, NSW).

DISTRIBUTION

P. gracilis has been recorded only from a narrow band of medium to low woodland on Quaternary coastal alluvium and granite north of Wharps Holding (S of Herbert River, Ingham) to the Hull River, a latitudinal range of almost 80km (Fig. 1). In this band, *P. gracilis* has been found at altitudes below 90m a.s.l. with most records from between the 0-20m contours (Tables 1 and 2).

RESULTS

HABITAT

Vegetation associated with *P. gracilis* included Vegetation Types 15a (Medium Open-forest i.e. paperbark swamp), 17 (Coastal Beach Ridges and Swales), 19 (Coastal Floodplains and Piedmont slopes), 20 (Texture-contrast Soils with Impeded Drainage on Coastal Plains) and 24 (Cleared) of Tracey (1982). The appropriate Tracey vegetation type (TVT) appears with each site vegetation proforma below. The following abbreviations were used to describe the relative abundance of plant species (A-abundant, C-common, O-occasional, U-uncommon).

Sites marked thus * indicate records supplied courtesy of Queensland Forest Service. Tracey (1982) provides an overview of climate, physiography, geography and soils of the area. The Quaternary lowland coastal plains and extensive

beach ridges which typify the distribution of *P. gracilis* occur in narrow corridors up to 10km wide and 50km long between the steep ranges near the coast and the main scarp further upland. Soil types are determined by drainage; on the better-drained levees yellow friable loams predominate, and there is a progression to gleyed podzolic soils, humic gleys and acid peats as the site drainage becomes poorer. Calcareous or siliceous sands are found on the younger near-coastal ridges and podzols occur on the older ridges.

Annual rainfall is high, but widely different rainfall regimes operate and vary considerably over short distances because of local topographic changes which include the height and orientation of mountain ranges and the direction of the coastline with respect to the prevailing south-east air stream. The wide coastal plains and beach ridges show dramatic drops in rainfall from coast to foothills, e.g. Halifax 2127mm west to Upper Stone 1533mm in 45km. The relative dryness of foothills and eastern slopes may account for the apparent restriction of the glider to areas of very low elevation (below 90m a.s.l.). While foothills may receive only slightly less summer rainfall than coastal plains (Rollingstone, 19°03'S 146°24'E, Dec 220mm, Jan 416mm, Feb 344mm compared with coastal plain Euramo, 18°00'S 145°56'E Dec 167mm, Jan 597mm, Feb 652mm), dry season rainfall in foothills may be inordinately low (Rollingstone Jun 15mm, Jul 11mm, Aug 18mm, Sept 25mm contrasted with Euramo Jun 132mm, Jul 93mm, Aug 67mm, Sept 99mm). Latitudinal variation in rainfall may also be dramatic over short distances, e.g. Tully 4188mm south to Cardwell 2132mm in 40km.

SITE RECORDS (see Table 1)

Two historic records exist for which there can be no precise fix:

i. 'North of Cardwell' (de Vis 1883). No habitat information is included in the original description, and to date no Broadbent diary has been found for that period. The Edmund Kennedy National Park (NP 771) now accounts for approximately 6200ha of largely unaltered lowland coastal land immediately north of Cardwell (to the Murray River). The park contains a variety of lowland vegetation communities (all below 20m elevation) from mangroves, bulkuru swamps, paperbark forest and dry eucalypt woodland through to rainforest. Approximately 30% of this park could be considered possible habitat for *P. gracilis* (open sclerophyll forest with shrubby

understorey), approximately 1% could be considered optimal habitat. The glider has recently been recorded within the park boundary. For more detailed floristics see habitat data (for sites 13 and 14) below.

ii. 'Mt Echo' (locality information on tags attached to skins JM5521, JM5522, JM5523). No specific vegetation or elevation information is available with this record and although the 1886 diary of Kendall Broadbent documents his camp on the Herbert River and his collecting efforts on the steep slopes and summit of Mt Echo, no details are given concerning where gliders were collected. The problem is further compounded by Broadbent's various references to vernaculars such as 'small flying squirrels', 'flying squirrels', and a 'large flying squirrel' in lieu of specific titles for collected examples of *Petaurus breviceps*, *P. gracilis* and *Petauroides volans*. Vegetation of the dry slopes of Mt Echo beside the Herbert R has probably changed little since Broadbent's day. At one site (18°24'52"S 145°46'13"E) the dominant species in the upper canopy (23m with 30% cover) were *Eucalyptus tereticornis* (C), *Lophostemon suaveolens* (A), *E. clarksoniana* (O) and *E. tessellaris* (O). Understorey (<5% cover) species comprised *Planchonia careya* (O) and *Pandanus* sp. (O). Ground layer (100% cover) consisted of *Imperata cylindrica*, *Mnesithea rotboelliioides* (A), *Trumfetta rhomboidea* (C) and *Panicum maximum* (O). Soil was rocky, brown sandy loam, TVT 19.

Contemporary records for which more precise fixes are available (Fig. 1):

1. *Wharps Holding (18°41'18"S 146°04'25"E). Dominant species of the upper stratum (25m with <45% cover), *E. platyphylla* (U) and *Metaleuca dealbata* (A). Understorey (20% cover) composed of *L. suaveolens* (C) and *Pandanus* sp. (U). Ground layer (50% cover and heavily grazed) probably *I. cylindrica* and other grasses. This area was notable for its coarse mosaic of single species associations. Isolated clumping of single species included *M. dealbata*, *L. suaveolens*, *E. tessellaris* and *Acacia crassicaarpa* with *E. platyphylla* scattered throughout. This area is renown for its protracted periods of extensive inundation during the wet season. Soil, grey loam, TVT approaching 16p. A second glider observation was made nearby (100m N) on a gently sloped rocky ridge (40m a.s.l.) where dominant species of the upper stratum (18m with <30% cover) included *E. platyphylla* (O), *L. suaveolens* (A), *E. tessellaris* (O) and *E. dolichocarpa*. The understorey (<1% cover) was com-

TABLE 4. Species, numbers, dimensions and densities of trees at four *P. gracilis* nest sites. CBH=circumference at breast height.

Nest Site	Total No. trees	Tree species	Number on grid (% of all trees)	Mean number /1000 m	Height range (m)	Mean Ht (m), (SD), (SE)	CBH range (mm)	CBH mean, (SD), (SE)
1. Barretts Lagoon 18°01'33"S, 145°59'08"E <i>E.intermedia</i> (live) Ht 7m, CBH 780mm Surveyed 13.8.91 Fig. 11.	1204	<i>Eucalyptus intermedia</i>	31 (2.6)	17.2	3-10	7.10 (2.13) (0.69)	160-940	554.61 (224.32) (7.24)
		<i>E. pellita</i>	1 (0.08)	0.5	10	10.00	730	730
		<i>Lophostemon suaveolens</i>	26 (2.2)	14.4	3-9	6.11 (2.23) (0.09)	110-920	447.69 (254.36) (9.78)
		<i>Acacia crassicaarpa</i>	21 (1.7)	11.7	3-8	4.76 (1.58) (0.07)	110-650	252.86 (154.89) (7.38)
		<i>A. flavescens</i>	3 (0.2)	1.7	3	3.00	100-130	113.33 (15.27) (5.09)
		<i>A. pubirhachis</i>	1 (0.08)	0.5	3	3.00	100	100
		<i>Melaleuca viridiflora</i>	69 (5.7)	38.3	3-8	4.23 (1.41) (0.02)	70-670	270.88 (154.01) (2.23)
		<i>Pandanus citraceus</i>	34 (2.8)	18.9	<1			
		<i>Xanthorrhoea johnsonii</i>	1018 (84.5)	565.5	<1			
2. Barretts Lagoon <i>Scleria</i> swamp 18°01'44"S 145°59'04"E <i>E. pellita</i> (live) Ht 12m, CBH 1490mm Surveyed 14.8.91 Fig. 12.	466	<i>E. pellita</i>	17 (3.6)	9.4	3-13	9.00 (4.05) (0.24)	110-1650	709.41 (560.03) (32.93)
		<i>L. suaveolens</i>	52 (11.2)	28.9	3-14	6.79 (3.52) (0.07)	130-1590	501.35 (384.82) (7.40)
		<i>A. crassicaarpa</i>	4 (0.9)	2.2	5-12	7.25 (3.20) (0.80)	200-460	370.00 (197.15) (49.29)
		<i>A. flavescens</i>	1 (0.2)	0.5	3	3.00	110	110
		<i>M. quinquenervia</i>	176 (37.8)	97.8	3-14	8.68 (3.65) (0.02)	110-1940	513.01 (304.86) (1.732)
		<i>Melicope elleryana</i>	3 (0.6)	1.7	3	3.00	100-150	120.00 (26.46) (8.82)
		<i>Deplanchea tetraphylla</i>	1 (0.2)	0.5	12	12.00	780	780
		<i>P. citraceus</i> >1m	19 (4.1)	10.5	2-10	5.89 (2.86) (0.15)	430-650	542.63 (65.22) (3.43)
		<i>P. citraceus</i> <1m	43 (9.2)	23.9	<1			
		<i>Gahnia sieberiana</i>	131 (28.1)	72.8	<3			
		<i>X. johnsonii</i>	18 (3.9)	10.0	<1			
3. Barretts Lagoon "Ricefields" 18°01'26"S 145°58'46"E <i>L. suaveolens</i> (live) Ht 10m, CBH 1250mm Surveyed 15.8.91 Fig. 13.	690	<i>E.intermedia</i>	18 (2.6)	10.0	3-12	7.00 (2.30) (0.13)	120-840	408.89 (205.57) (11.42)
		<i>E. pellita</i>	37 (5.4)	20.5	3-15	6.89 (3.93) (0.11)	70-3000	589.02 (760.50) (20.55)
		<i>L. suaveolens</i>	73 (10.6)	40.5	3-10	5.49 (2.10) (0.03)	60-1400	375.30 (305.34) (4.18)
		<i>M. viridiflora</i>	6 (0.9)	1.7	3-6	4.33 (1.03) (0.17)	90-550	241.67 (149.45) (24.91)
		<i>M. dealbata</i>	1 (0.1)	0.5	6	6.00	300	300.00
		<i>A. crassicaarpa</i>	11 (1.6)	6.1	3-9	6.36 (1.80) (0.16)	80-700	428.18 (200.64) (10.61)
		<i>A. flavescens</i>	2 (0.3)	1.1	3-4	3.5 (0.70) (0.35)	150-180	165.00 (21.21) (10.61)
		<i>Planchonia careya</i>	1 (0.1)	0.5	4	4.0	210	210.00
		<i>P. citraceus</i> >1m	15 (2.2)	8.3	2-6	3.93 (1.03) (0.07)	280-450	350.00 (50.00) (3.33)
		<i>P. citraceus</i> <1m	272 (39.4)	151.1	<1			
		<i>X. johnsonii</i>	245 (35.5)	136.1	<1			
4. Barretts Lagoon 10°01'35"S 145°58'52"E Dead stag Ht 13m, CBH 1620mm Surveyed 16.8.91 Fig. 14.	680	<i>E. intermedia</i>	38 (5.6)	21.1	3-14	8.45 (3.29) (0.09)	70-1940	509.21 (370.20) (9.74)
		<i>E. pellita</i>	29 (4.3)	16.1	3-14	7.65 (3.99) (0.14)	50-1040	425.51 (344.78) (11.89)
		<i>L. suaveolens</i>	51 (7.5)	28.3	3-12	5.84 (2.65) (0.05)	90-10000	293.92 (205.76) (4.03)
		<i>M. dealbata</i>	2 (0.3)	1.1	2-4	7.00 (4.24) (2.120)	130-520	325.00 (275.77) (137.89)
		<i>A. crassicaarpa</i>	33 (4.8)	18.3	3-10	6.00 (2.60) (0.08)	60-670	284.54 (188.65) (5.72)
		<i>A. flavescens</i>	27 (4.0)	15.0	3-12	7.15 (2.75) (0.10)	60-740	328.15 (199.19) (7.38)
		<i>P. careya</i>	2 (0.3)	1.1	3-4	3.50 (0.71) (0.35)	200-240	220.00 (28.28) (14.14)
		<i>P. citraceus</i> >1m	3 (0.4)	1.7	2-6	4.67 (2.31) (0.77)	320-490	406.67 (85.05) (28.35)
		<i>P. citraceus</i> <1m	84 (12.3)	46.7	<1			
		<i>X. johnsonii</i>	411 (60.4)	228.3				

Additional notes on nest sites of Table 4.

Understorey.

Site 1 (Fig. 11): Dry low woodland between swale with groundcover sparse, homogeneous throughout with 70-95% cover and dominated by *Themeda triandra* and *Leptocarpus ramosus* (both about 1 m) with smaller representation (< 10 specimens) by *Lomandra longifolia*, *Dianella caerulea*, *Melastoma affine*, *Banksia integrifolia* var. *aquilina*, *Dipodium ensifolium*, *Schoenus sparteus* and *Lindsaea ensifolia*. Regrowth (< 3 m) with 10-20% cover by *Acacia mangium*, *A. crassicarpa*, *Lophostemon suaveolens*, *E. pellita*, *M. viridiflora* and *A. pubirhachis*. Of *X. johnsonii*, (tallest 800mm), 32 with green scapes (7 with *P. gracilis* foot prints, 2 with gouges), 130 with dry seeded scapes. Site 1 sufficiently elevated to escape inundation in wet season.

Site 2 (Fig. 12): Tall teatree-razorgrass swamp with eastern edge encroaching swale and dominated by dense groundcover (90%) of *Leptocarpus ramosus*, *Blechnum indicum*, *Scleria ciliaris*, *Baumea* sp., and *Ischaemum australe* var. *villosum*. Sparse cover of *M. affine*. Southern and western quarters dominated by *S. ciliaris* and *B. indicum* to 1400mm (70-90%), *Baumea* sp. (approx 2%) and *Dichranopteris linearis* (approx 5%). The drier, more elevated western quarter dominated by *I. australe* var. *villosum* and *L. ramosus* at 400mm (approx 50%) with *Gahnia sieberiana* at 1.2m (10%), *D. linearis* at 600mm (5%) and stunted *M. quinquenervia* (2%) with *L. ramosus* at 600mm and *Eracaulon australe* at 300mm in the swale. Sparse (<1%) regenerating vegetation comprised *M. quinquenervia* in western, southern and eastern quarters with *Acrassiacarpa*, *A. flavescens* and *L. suaveolens* (total 2%) in the north. *X. johnsonii* showed 4 green scapes, 4 dry seeded scapes, 1 with foot prints and 0 scarred.

Site 3 (Fig. 13): Swale and medium to low woodland. Southern half (swale) dominated by dense groundcover (75% cover) of stunted *M. quinquenervia* (5-6%) at 0.5m, *M. viridiflora* (30 specimens all < 3 m), *I. australe* var. *villosum* (80%) at 1.1 m, *Themeda triandra* (1-5%), *Leptocarpus ramosus* (5%), *Scleria polycarpa* (5%) and *Eriachne triseti* (5%). Northern half (woodland) densely covered (100%) with *I. australe* var. *villosum*, *T. triandra* and *Lomandra longifolia*, *Smilax australis* abundant and up to 4 m, *L. ensifolia* common in localised clumps, *M. affine* sparse, *D. caerulea* common, *Planchonia careya* common and up to 3 m, *M. affine* to 2m but uncommon, *Schoenus calystachyus* common. Vegetation dominated by *A. flavescens* to 3m and spaced at approximately 2 m, *A. crassicarpa* to 3m but less common. *X. johnsonii* showed 41 green scapes, 58 dry seeded scapes, 11 with foot prints and 5 scarred.

Site 4 (Fig. 14): Groundcover homogeneous throughout with *Smilax australis* rampant and up to 6 m. *L. ensifolia* common throughout, *H. actiuigilum* sparse, *D. caerulea* common, *Pteridium esculentum*, *T. triandra*, *P. careya*, *Schizaea dichotoma* sparse, *Eustrephus latifolius*, *L. longifolia* common, *Clerodendrum longiflorum* var. *cunninghamii* common to 2m and often dense. *M. affine* forming clumps up to 2m high by 12m wide, *Alphatonia excelsa* sparse. Regenerating *A. flavescens* and *A. crassicarpa* to 3m common and forming 20% cover. Many dead acacias 8-10 m. *X. johnsonii* showed 80 green scapes, 131 dry seeded scapes, 51 with foot prints and 23 scarred.

posed of *Planchonia careya* (O) and the ground layer (50% cover and heavily grazed) of probably *I. cylindrica* and other grasses.

2 & 3. *Tinkle Creek (18°39'20"S, 145°54'55"E) and *Lannercost Creek (18° 38'20"S, 145°54'15"E). Dominant species in the upper canopy (22m with 30% cover), *E. platyphylla* (C), *E. clarksoniana* (C), *E. tessellaris* (C) and *E. drepanophylla* (C). Understorey (30% cover) composed of *P. careya* (C) and *Xylomelum scollium*. Ground layer (50% cover and grazed) of *Cajanus reticulata* and *Heteropogon contortus*. Soil, coarse pale sand and rocks, TVT 16p. Foot-hills with a gentle slope (1:10).

4. Ashton Creek (18°37'41"S, 145°53'57"E). Glider not seen feeding. Dominant species in the upper canopy (24m with 35% cover), *E. tereticornis* (C), *E. platyphylla* (C), *E. clarksoniana* (C) and *E. tessellaris* (C). Understorey (20% cover) composed of *P. careya* (C), *A. crassicarpa* (O), *A. mangium* (O), *L. suaveolens* (O), *Albizia canescens* (U) and *Timonius timon* (U). Ground layer (50% cover and grazed) of *Hypis*

capitata, *I. cylindrica* and other grasses. Soil, brown sandy loam, TVT 20.

18° 37'26"S 145° 54' 12"E. Gliders feeding in flowering *E. tereticornis*. Dominant species in the upper canopy (20m with 35% cover), *E. tereticornis* (C), *L. suaveolens* (A), *E. clarksoniana* (O), *E. tessellaris* (O), *A. crassicarpa* (O) and *Acacia mangium* (O). Understorey (<5% cover) of *P. careya* (O). Ground layer (30% cover and heavily grazed) of unidentified grasses. Soil, grey-brown sandy loam, TVT 20.

5. Lannercost Creek (18°37'13"S, 145°56'44"E) (tongue of natural vegetation between exotic pine plantation and creek). Glider not seen feeding. Dominant species in the upper canopy (30m with 30% cover), *E. drepanophylla* (C), *E. dolichocarpa* (O), *L. suaveolens* (O), *E. tessellaris* (O), *E. platyphylla* (U) and *M. leucadendron* (C) on the creek. Understorey (10% cover) composed of *P. careya*, *Acacia crassicarpa*, *A. mangium* (creek), *Carallia brachiata* and *Dillenia alata*. Ground layer (60% cover and heavily grazed) of probably *I. cylindrica* and other un-

identified grasses. Soil, grey-brown loam, TVT 20

6. **Elphinstone Creek** (18°29'42"S, 146°01'26"E) (isolated *E. clarksoniana* on edge of cane field with remnant creek vegetation). Glider feeding on *E. clarksoniana* blossom. Dominant species in the upper canopy (20m with 30% cover), *L. suaveolens* (C), *E. platyphylla* (C) and *E. clarksoniana* (C). Understorey (<10% cover) composed of *P. careya* (C) and *A. crassicaarpa* (C). Ground layer (80% cover) of *I. cylindrica* and *Themeda triandra*. Soil, grey-brown sandy loam, TVT 19.

7. **Porters Creek** (18°26'57"S, 146°07'35"E). Glider feeding on blossom of *E. pellita*. Gully with 20m buffer zone, bordered both sides by exotic pine plantation. Dominant species of the upper stratum (25m with 50% cover), *E. intermedia*, *E. pellita*. Understorey (30% cover) composed of *Casuarina torulosa* (C, almost forming canopy), *A. flavescens* (C), *A. crassicaarpa* (O), *X. scottianum* (O), *A. mangium* (O), *P. careya* (C) and *Persoonia falcata* (O). Ground layer (60% cover) of *T. triandra*, *Pteridium esculentum*, *Lomandra longifolia* (C), *Mnesithea rottboellioides* (C). Soil, brown, sandy loam, TVT 16f (without *Syncarpia glomulifera* and *Banksia compar*).

18°26'47"S, 146°07'17"E. Glider not seen feeding. Dominant species of the upper stratum (25m with 50% cover), *E. clarksoniana* (C), *E. platyphylla* (C) and *Lophostemon suaveolens* (C). Understorey (20% cover) composed of *A. flavescens* (A) and *A. mangium* (O). Ground layer (60% cover) of *H. triticeus* (O), *T. triandra* (C) and *I. cylindrica* (A). Soil, grey-brown, sandy loam, TVT 19.

8. **Mullers Creek** (18°26'13"S, 146°07'15"E). Gliders not seen feeding, site logged and thinned

out. Dominant species of the upper stratum (20m with 30% cover), *E. clarksoniana* (C), *E. platyphylla* (C), *L. suaveolens* (C), *E. tessellaris* (O), *Melaleuca dealbata* (O), and *Albizia canescens* (O). Understorey (<5% cover) composed of young *M. dealbata*. Ground layer (80% cover) of *T. triandra* (C) and *I. cylindrica* (A). Soil, grey-brown loam, TVT 19.

9. **Lumholtz National Park** (18°24'30"S, 145°46'10"E (rainforest transition site by the Herbert R). Glider feeding on *Melicope elleryana* blossom. Dominant species in the upper canopy (22m with 50% cover), *E. tereticornis* (C), *M. elleryana* (O), *L. suaveolens* (C), *Aleurites moluccana* (O), *Lauraceae* sp. (O), and *E. torelliana*.

Understorey (40% cover) composed of *Mallothus philippinensis* (O), *Macaranga tanarius* (O), *Aphananthe philippinensis* (O), and *Lantana camara* (O). Ground layer (10% cover) of *Calamus caryotoides* and *Trumfetta rhomboidea*. Soil, brown sandy loam, TVT 19.

10. ***Cement Creek** (18°23'55"S, 146°05'57"E). Site not surveyed.

11. **Kennedy Valley** (18°13'31"S, 145°55'23"E). Site presumed. Closest woodland stand to location of specimen snared on barbed-wire fence. Dominant species of the upper stratum (22m with 40% cover), *E. tereticornis* (C), *E. pellita* (C), *E. drepanophylla* (C), *E. clarksoniana* (O), *Acacia mangium* (C) and *E. tessellaris* (U). Understorey (30% cover) composed of *A. flavescens* (C), *Pandanus* sp. (O), *Guioa acutifolia* (O), *Breynia cernua* (O) and *L. camara* (C). Ground layer (40% cover) of *T. triandra* (C) and *I. cylindrica* (A). Soil, brown loam, TVT 20.

12. **Baird Creek** (18°12'11"S, 145°58'17"E). Glider feeding on *E. tereticornis* blossom. Dominant species of the upper canopy (25m with 40% cover), *E. tereticornis* (C), *E. clarksoniana* (C),



FIG. 11. Vegetation surrounding Nest Site 1 (of Table 4), Barretts Lagoon. Den tree is arrowed

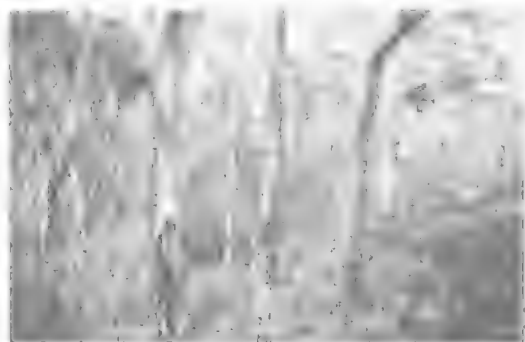


FIG. 12. Vegetation surrounding Nest Site 2 (of Table 4), Barretts Lagoon. Den tree is arrowed.

A. mangium (C), *E. tessellaris* (O), *Melaleuca dealbata* (O) and *Melicope elleryana* (O). Understorey (50% cover) composed of *Alphitonia excelsa* (C), *Glochidion ?lobocarpum* (C), *B. cernua* (C), *Acacia flavescens* (C), *Polyscias elegans* (C) and *Planchonia careya* (O). Ground layer (<5% cover) of *Alpinia caerulea* (U) and *I. cylindrica* (U). Soil, grey-brown loam, TVT 19.

13. **Edmund Kennedy National Park** (18°12'04"S, 145°59'14"E). Glider not seen, call only recorded. Dominant species of the upper canopy (25m with 45% cover), *E. tereticornis* (C), *Acacia mangium* (C), *Lophostemon suaveolens* (C), *E. tessellaris* (U), *Melaleuca dealbata* (O) and *E. intermedia* (O). Understorey (30% cover) composed of *Alphitonia excelsa* (O), *G. ?lobocarpum* (C), *A. crassicaarpa* (C), *P. elegans* (C), *D. alata* (C) and *Pandanus* sp.(O). Ground layer (30% cover) of *I. cylindrica* (A), *Pteridium esculentum* (O), *T. triandra* (O), *Cycas media* (U), *Heteropogon ?triticeus*, with *Cymbidium madidum*, *Platyrrhynchus hillii* and *Smilax australis* (C). Soil, grey sand, TVT 19.

18°08'43"S, 145°57'50"E. Although this glider was recorded east of (and hence inside) the Edmund Kennedy National Park fence line, the site does not actually occur within the National Park. The fence does not accurately reflect the gazetted east-west boundary. Glider not seen, call only recorded. Dominant species of the upper canopy (20m with 35% cover), *E. pellita* (A), *E. intermedia* (C), *L. suaveolens* (O) and *Deplanchea tetraphylla* (U). Understorey (30% cover) composed of *A. flavescens* (C), *A. crassicaarpa* (C) and *Dillenia alata* (O). Ground layer (40% cover) of *Melastoma affine* (C), *Gahnia sieberiana* (O) and *Scleria ciliaris* (A). Soil, grey sandy loam, TVT 19.

Glider moved from this site into adjacent tea-tree swamp where the dominant species of the upper canopy (15m with 50% cover) was *Melaleuca quinquenervia*. Ground layer (95% cover) of *Melastoma affine* (C), *G. sieberiana* (O), *A. pubirhachis* (C), *Rhynchospora* sp. (C), *Schoenus ?melanocephalus* (C), *Lycopodium cernuum* (O), *Leptocarpus ramosus* (A), *Eriocaulon* sp. (A), *Ischmaeum* sp. (C) with *Drosera spatulata*, *Myrmecodia beccarii* and *Dischidia nummularia*. Soil, grey sandy loam, TVT 15a.

14. **Dalachy Creek** (18°09'26"S, 145°57'26"E). Glider feeding on flowering *E. clarksoniana* in cleared paddock. Vegetation proforma of closest adjacent site (creek community). Dominant species of the upper canopy (20m with 80% cover), *A. mangium* (C), *A. dulacarpa* (C), *L.*

phostemon suaveolens (C), *Tristaniopsis exiliflora* (C), *Eucalyptus intermedia* (U). Understorey (30% cover) composed of *Alstonia muelleri*, *Polyscias elegans* and *P. australiana*. Ground layer (<1% cover) of *Piper novae-hollandiae*, *Lygerdium* sp., *Tetracera nordiana* and *Lomandra hystrix*. Soil, brown loam, TVT 24 (cleared near TVT 1a).

18°08'51"S, 145°57'40"E. Glider feeding on flowering *E. pellita*. Dominant species of the upper canopy (20m with 30% cover), *E. pellita* (C). Understorey (40% cover) composed of *Lophostemon suaveolens* (C), *Acacia flavescens* (C), *A. crassicaarpa* (C), *Dillenia alata* (O), *Pandanus* sp. (C) and *Melaleuca quinquenervia* (C). Ground layer (30% cover) of *Scleria ciliaris* (A) and *Blechnum indicum* with *Dendrobium smilae* and *Drynaria rigidula*. Soil, grey-brown sandy loam, TVT 19.

15. **Murray Upper** (18°08'38"S, 145°47'54"E). Rainforest transition site, gully with 20m buffer zone, bordered both sides by pine plantations, glider not recorded feeding. Dominant species in the upper canopy (20m with 40% cover), *E. pellita* (C), *E. clarksoniana* (C), *A. mangium* (C), *E. tessellaris* (C) and *L. suaveolens* (C). Understorey (70% cover) composed of *A. flavescens* (C), *Guioa acutifolia* (O), *Scolopia braunii* (C), *Timonius timon* (C), *Dillenia alata* (C), *Rubus moluccanus* (C) and *Polyscias australiana* (C). Ground layer (<2% cover) of *Smilax australis* (C), *Hysperpalaurina* sp. (C) and *Lomandra longifolia*. Soil, brown sand, TVT 19.

16. **Bilyana** (18°07'S, 145°56'E). Mounted specimen in private collection of T. Marsilio for which the only collection details (from card attached to specimen) are as follows: 'Fly Squerrel was killed in falling tree in front of Joe Ottone while Alec was clearing line for El. Power. at Bilianna on Bluff Road. 15 ?years ago'. TVT 24 with remnants of 19.

17. ***Murray Upper** (18°06'30"S, 145°49'40"E). Dominant species of the upper canopy (25m with 40% cover), *E. tereticornis* (C), *A. mangium* (C), *E. tessellaris* (O), *M. dealbata* (O), *E. clarksoniana* (C) and *Melicope elleryana* (O). Understorey (50% cover) composed of *Alphitonia excelsa* (C), *Glochidion ?lobocarpum* (C), *A. flavescens* (C), *Polyscias elegans* (C), *Breynia cernua* (C) and *Planchonia careya*. Ground layer (<5% cover) of *I. cylindrica* (U) and *Alpinia caerulea* (U). Soil, grey-brown sand, TVT 19.

18. **Yingalinda Beach** (18°03'18"S, 146°01'37"E). Glider recorded in *E. intermedia*. Dominant species in the upper canopy (35m with 35%

cover), *E. intermedia* (C) and *L. suaveolens* (C). Understorey (40% cover) composed of *A. flavescens* (A), *A. crassicarpa* (A), *Polyscias elegans* (O), *Alstonia muelleri* (O), *Canarium australiana* (O), *Deplanchea tetraphylla* (O) and *Planchonia careya*. Ground layer (20% cover) of *Scleria sphaolata* (C), *Pteridium esculentum* (C), *I. cylindrica* (C) and *Xanthorrhoea johnsonii* (O) with *Smilax australis*, *Eria fitzalanii*, *Dendrobium smilliae* and *Cymbidium madidum*. Soil, grey sand, TVT 17.

19. **Barretts Lagoon.** (i) South western bank (18° 02'31"S, 145° 58'36"E). Gliders recorded feeding on flowering *Eucalyptus tessellaris*. Site cleared Feb 1990. Prior to that the dominant species in the upper canopy (35 m) were *E. pellita*, *E. intermedia*, *Acacia mangium*, *E. tessellaris*, *E. tereticornis* and *L. suaveolens*. Understorey (9m and 80% cover) composed of regenerating *A. flavescens*, *Planchonia careya*, *A. crassicarpa*, *Melastoma affine*. Ground layer (20% cover and grazed) of *I. cylindrica* and *Themeda triandra*, *S. australis* and *Lomandra longifolia*. Soil, grey sand, TVT 24 with remnants of 17.

(ii) North eastern bank (18°02'22-23"S, 145°58'52"E). Gliders recorded feeding and heard grunting in flowering *E. tereticornis*. Remnant vegetation along immediate edge of Barretts Lagoon. Isolated specimens (to 30m) of *A. mangium*, *E. tessellaris*, *L. suaveolens*, *M. leucadendron* and *M. dealbata*. TVT 24.

(iii) 'Rice Fields' (18°01'26"S, 145°58'46"E). Gliders feeding in *E. pellita*, *E. intermedia*, *L. suaveolens*, *X. johnsonii*. See detailed vegetation analysis 'Nest site 3', Table 4. TVT 17.

(iv) East (18°01'33"S, 145°59'34"E). Gliders feeding in *X. johnsonii* and *M. dealbata*. Dominant species in the upper canopy (20m with 50% cover), *E. pellita* (C), *E. intermedia* (C), *L. suaveolens* (C), *A. crassicarpa* (C), *M. dealbata* (O), *Deplanchea tetraphylla* (U). Understorey (30% cover) composed of *A. flavescens* (C), *M. viridiflora* (C), *Banksia integrifolia* var. *aquilina* (U), *Casuarina littoralis* (C) and *Pandanus* sp. Ground layer (40% cover) of *T. triandra* (C), *L. longifolia* (C), *Lindsaea ensifolia* (A), *Leptocarpus ramosus* (A) and *X. johnsonii* (A). In wetter gullies at base of swales, dominant canopy species (18-20m with 50% cover) changed to *E. pellita* (A), *Lophostemon suaveolens* (A) and *A. mangium* with an understorey (15% cover) of *A. flavescens* (O), *A. crassicarpa* (O), *Pandanus* sp.(O) and *Dillenia alata*. Ground layer (30% cover) of *Gonocarpus ?acanthocarpus* (C), *Lindsaea ensifolia* (C), *Dicranopteris linearis* (O),

Melastoma affine (C), *Eriocaulon* sp., *Scleria laevis* (C), *Ishmaeum australe* (A), *Flagellaria indica* (O) with *Eria fitzalanii* and *Dendrobium smilliae*. Soil, dark brown sandy loam, TVT 17.

20. **Hull River** (17°58'29"S, 146°02'02"E). Glider feeding in *E. intermedia*. Dominant species of the upper stratum (30m with 40% cover), *Eucalyptus intermedia* (C), *E. pellita* (A), *A. mangium* (C), *Lophostemon suaveolens* (O) and *Deplanchea tetraphylla* (O). Understorey (70% cover) composed of *Davidsonia pruriens* (C), *Polyscias australiana* (C), *A. muelleri* (C), *Dillenia alata* (O), *Wilkiea nuegeliana* (C), *Rhodomertus* sp., *Pandanus* sp., *Syzygium wilsonii*, *Lepidozamia hopei*, and *A. flavescens* (A). Ground layer (<10% cover) of *Calamus caryotoides*, *C. moti*, *Smilax australis*, *F. indica*, *Lygopodium* sp., with *Eria fitzalanii*, *Dendrobium smilliae*, *Cymbidium madidum* and *Platycorys hillii*. Soil, brown sand to sandy loam, TVT 17 adjacent to TVT 15a.

SPOTLIGHTING

Spotlighting surveys for *P. gracilis* were conducted at a number of sites (Table 3). The species was recorded at 16 of the 36 localities and represented a total of 1334 manhours of observation. In habitats supporting *P. gracilis*, the most commonly observed arboreal marsupial assemblage comprised *P. gracilis*, *Dactylopsila trivirgata*, *P. breviceps* and *Acrobates pygmaeus*. The presence of this group of exuvivores and insectivores and the obvious absence of such foliovores as *Trichosurus vulpecula*, *Pseudocheirus peregrinus*, *Petauroides volans* and *Phascogale cinereus* may have been a reflection of possible nutritional deficiency in vegetation of the coastal alluvium, however this was not addressed in the study.

Trichosurus vulpecula was extremely rare in habitat considered optimal for *P. gracilis*. Only 1 specimen of the brushtail was recorded near such habitat (Dalachy Creek) and at that site *T. vulpecula* was recorded from a tree isolated in improved (fertilised) pasture. Where *T. vulpecula* occurred commonly with *P. gracilis* (e.g. Wharps Holding) the habitat was considered marginal or poor for the glider.

BIOCLIM PREDICTION

A climate profile (Table 5) was generated by the BIOCLIM prediction system (see Nix & Switzer, 1991) after completion of field surveys. Using core predictions [geographic points matching all 28 climatic values (7 for radiation, 7 for

temperature, 7 for precipitation and 7 for moisture index) between the 5% and 95% values (the 90 percentile range) in the climate profile] the presence of *P. gracilis* was predicted beyond that area encompassed by the field results presented in Table 1 only on the north western tip of Hinchinbrook Is. (Fig. 15). Soils of the north western tip developed in situ largely from massive rhyolitic to dacitic volcanics and to a much lesser extent riebeckite granite near Scraggy Point. The north western lowland woodland communities there do not reflect a mirror image of the woodlands of the Coastal Floodplains and Piedmont Slopes (TVT 19) across the Hinchinbrook Channel on the mainland. Many potential sites (TVT 13e, 15b) appeared to be losing their identity under the encroachment of rainforest species, and drier forest types tended to be dominated by *Eucalyptus clohesiana* which grew from near sea level to well above the 100m contour. To date *P. gracilis* has not been recorded from *E. clohesiana*. In Sept 1992 two nights were spent surveying in woodland slopes supporting *E. intermedia*, *E. clohesiana*, *E. tessellaris*, *E. acmenoides*, *Melaleuca leucodendron*, *Pandanus* sp. and *Xanthorrhoea johnsonii* (Table 3) without success. Hinchinbrook Is. should be resurveyed for *P. gracilis*.

Using marginal predictions (all 28 climate values falling within the total range in the climate profile) *P. gracilis* was again only predicted to occur inside the core area plotted for the north west tip of Hinchinbrook Is.

TRAPPING

A total of 721 trapnights resulted in the capture of one *P. breviceps* from degraded habitat being cleared at Barretts Lagoon (16 Feb 1991). No *P. gracilis* were collected by this method in spite of the trapping program being conducted under the on-site advice of field researchers skilled at capturing other petaurids such as *P. breviceps*, *P. australis* and *P. norfolcensis*. The degree of difficulty in trapping *P. gracilis* by traditional methods greatly impinges on the understanding of its social organisation which is fundamental to the process of estimating its population density.

ARTIFICIAL HOLLOWES

Two sub-adult female *P. gracilis* (ear tagged T4027, T4028) were caught together in 'nestbox' No. 8 on 10 May 1991. No other *P. gracilis* were trapped by this method but other individuals were known to use the tubes e.g. radio-tagged adult male T4030 was recorded once (7 Aug 1991) in 'nestbox' 12, and an unmarked adult male (pos-

sibly T4030) escaped from 'nestbox' 27 before the entrance could be reached and plugged (4 Aug 1991). Subadult female T4028 used 'nestbox' 12 and 13 on 5 days during the period 11-19 May 1991. Tubes were more frequently inhabited by Brown Tree-snakes (*Boiga irregularis*), Green Tree Ants (*Oecophylla smaragdina*) and less frequently by Sugar Gliders (*P. breviceps*) (adult male and female, 'nestbox' 14, 25 May 1992; group in 'nestbox' 7 (east), 8 Oct 1992).

HOME RANGE DETERMINATION

Shortcomings associated with this part of the study are referred to under 'Methods'. Results of home range analysis and plots of dens appear in Figs 16-19. The 95% isopleth of the harmonic mean distance minimum gave a value of 23.01ha for adult female T4026 (110 fixes), 9.04ha for sub-adult female T4027 (36 fixes) and 13.86ha for sub-adult female T4028 (36 fixes). These results should be taken as preliminary and minimal as the plots indicate that the curves have not quite asymptoted (see Quin et al., 1992; Goldingay, 1992). Areas estimated using the minimum convex polygon (MCP) were 18.65, 16.48 and 10.96ha respectively. Overlap is shown in Fig. 19. Possible underestimation of home range size could be partly or wholly offset by patches of treeless swale included in the estimates. Sub-adults T4027 and T4028 may have been dispersing offspring of T4026. Insufficient fixes were taken of adult male T4030 (who dislodged his transmitter after 3 nights) or female T4031 (for which den fixes only were taken) to allow estimation of home ranges. However, male T4030 was known to have moved between the home range of adult female T4026 and one of the dens of adult female T4031 (see 'Reproduction' and Fig. 19). Serial den use (Kehl & Boorsboom, 1984) was noted between adult female T4026 and sub-adult female T4028, adult male T4030 and sub-adult female T4028. Conjoint den use was noted between adult male T4030 and adult female T4026, adult male T4030 and adult female T4031, and between the two sub-adult females T4027 and T4028.

REPRODUCTION

Petaurus gracilis appears to give birth in the spring, although this pattern is complicated by the record of hairless young in the pouch of a female collected in mid-February and an observed September copulation involving a female known to be carrying two hairless pouch young.

Two adult females captured 5 and 9 Aug 1991



FIG. 13. Vegetation surrounding Nest Site 3 (of Table 4), Barretts Lagoon. Den tree is arrowed.

(T4026 and T4031 respectively) each carried two hairless pouch young. Young measured approx 35mm crown to cloaca. Females resisted attempts to examine pouch young by contracting muscles surrounding the pouch opening. By 26 Nov 1991 young of T4026 [T4032 (M) and T4033 (F)] weighed 65g and 69g (respectively) (see Table 2 and Fig. 20) and the pouch of T4026 was noted to be divided longitudinal into two halves by a thin septum (see Calaby, 1966 for description in *P. australis*). The right pouch side was thinly covered with long ginger-brown hairs and the left contained two elongated nipples, each 6mm long. Adult female T4031 was not recaptured. The pouch of adult female JM7290 collected 14 Feb 1973 contained two hairless young. The pouch of female JM8549 (which died ensnared on a barbed wire fence Oct 1990) contained one newly furred young JM8550 (43g). The right posterior corner of the pouch contained well developed mammary tissue, anterior to which (close to the body) was

a covering of long ginger hair. The single nipple measured 11mm.

The following copulatory behaviour was noted between female T4026 and male T4030 (both captured in *Lophostemon suaveolens* den, nest site 3 of Table 4, Sept 5 1991) at a time when female T4026 was carrying 2 hairless pouch young. Observations on 7 Sept 1991 commenced at 1900hrs with female motionless in *L. suaveolens* close to den. At 2030hrs, male T4030 appeared in tree 7 metres away from the tree in which the female was sitting. Both remained motionless until 2100hrs. The male then produced a soft but hoarse call resembling 'chew-chew-chew-chew' at which the female made immediate efforts to join him (but was interrupted by noise from observers on the ground). At 2226hrs the male glided to the female's tree. The female appeared to sniff and lick the male's rump (probably applying male scent as observed in *P. australis* by Henry & Craig, 1984; Russell, 1984) and followed him up the trunk to sit together in the canopy. The female then glided to a nearby large *E. pellita*, was followed by the male and the two remained motionless, 'curled up' around one another in the canopy until 0040hrs. The female then leapt to a nearby tree and was followed closely by the male. From 0057hrs to 0155hrs the two remained motionless in a 'ball' whereupon the male lunged at the female and the two copulated until 0217hrs. During copulation male and female adopted a vertical, head-down position on the trunk with the female's head pushed against an ant plant (*Myrmecodia beccarii*). The male thrust intermittently, grasping the female's dorsum in a position not unlike that adopted by young back-riding gliders newly emerged from the pouch. A neck bite was maintained by the male until the two separated, whereupon the male licked and groomed his penis. The female leapt to a nearby *E. pellita*, was followed by the male and the two sat closely and motionless until 0400hrs whereupon the female made bursts of 'glide-and-freeze' (thought not to be induced by the presence of observers) toward a den which was some way off and reached by 0545hrs. The male had lost interest in the female by 0400hrs and moved elsewhere. The male did not share the den occupied by female adult T4026, but shared an *E. intermedia* den occupied by another adult female, T4031 (with pouch young). This den could be reached over a minimum distance of approx 1.5km from where T4026 and T4030 separated.

The following night (8 Aug 1991) observation commenced with female T4026 at 1830hrs. At

TABLE 5. BIOCLIM climate profile for *Petaurus gracilis* in tropical north Queensland based on all Queensland Museum records and observations. Temperature (°C); precipitation (mm); radiation (MJ/m²/day); moisture index [0 (moisture totally limiting to growth) -1 (moisture non-limiting to growth)]. Seasonality (coefficient of variance for 12 monthly values as %).

CLIMATE PARAMETER	Min	Percentile		Max
		5	95	
Annual mean temperature	23.78	23.80	23.94	23.95
Coldest month mean minimum temperature	12.73	12.80	14.09	14.09
Warmest month mean minimum temperature	31.77	31.81	32.69	32.74
Annual range (mean max-mean min temperature)	17.67	17.71	19.89	20.01
Wettest quarter mean temperature	26.65	26.68	26.96	26.97
Driest quarter mean temperature	20.00	20.12	22.22	22.30
Seasonality (coefficient of variance)	11.87	11.90	13.04	13.08
Annual mean rainfall	1528.76	1572.11	3176.25	3262.96
Wettest month mean rainfall	345.24	352.32	628.63	628.63
Driest month mean rainfall	14.48	20.60	69.54	76.66
Annual range (wettest month-driest month)	323.59	331.48	557.40	560.36
Wettest quarter mean rainfall	1012.90	1033.28	1828.06	1828.06
Driest quarter mean rainfall	54.84	60.89	230.45	236.50
Seasonality (coefficient of variance)	80.63	83.05	104.24	104.85
Annual mean daily solar radiation	18.81	18.90	19.69	19.72
Highest monthly mean daily solar radiation	24.92	24.97	25.41	25.42
Lowest monthly mean daily solar radiation	13.46	13.57	14.52	14.56
Annual range of monthly mean daily solar radiation	10.66	10.74	11.14	11.47
Wettest quarter mean daily solar radiation	19.76	19.76	20.10	20.10
Driest quarter mean daily solar radiation	16.06	16.27	20.07	20.21
Seasonality (coefficient of variance)	17.84	18.12	19.79	20.63
Annual mean moisture index	0.63	0.64	0.92	0.92
Wettest month mean moisture index	1.00	1.00	1.00	1.00
Driest month mean moisture index	0.15	0.16	0.54	0.59
Annual range (wettest-driest month)	0.41	0.46	0.85	0.85
Wettest quarter mean moisture index	0.98	0.98	1.00	1.00
Driest quarter mean moisture index	0.25	0.31	0.86	0.87
Seasonality (coefficient of variance)	15.97	17.33	55.37	56.72

1930hrs the female began moving between trees with apparent resolve only to sit 'frozen' for extended periods then move off in the same manner. Male T4030 appeared in a nearby tree at 2318hrs. The female made soft 'chee-chee-chee' calls which brought the male into her tree. The two sat closely until 0200hrs (when observations were abandoned). The pair did not share a daytime den.

The next night (9 Aug 1991) the same pair were noted consorting (only) from 2305-0100hrs. Observations continued to 15 Aug 1991 but the pair were not seen to consort again.

DENNING (see Table 4)

A total of 19 dens were recorded at Barretts

Lagoon (see Figs 16-19). These varied from a dead stag of undetermined species (13m) to living examples of *E. intermedia* (8), *L. suaveolens* (2), *M. quinquenervia* (2), and *E. pellita* (6) up to 27m in height (Figs 11-14). In tall trees it was usually impossible to determine either the den entrance or the den position inside the trunk. In two cases (sites 1 and 3, Table 4), both were known. At site 1 (Figs 11 and 21) the den was made in a 7m living *E. intermedia*. The 50mm entrance hole was 5.8m above ground, the nest cavity approx. 200mm dia. and the nest of dried leaves approx 3m below the entrance. At site 3 (Figs 13 and 22) The den was made in a 10m living *L. suaveolens*. The 45mm entrance hole was 3.8m above ground, the nest



FIG. 14. Vegetation surrounding Nest Site 4 (of Table 4), Barretts Lagoon. Den tree is arrowed.

cavity approx. 250mm diameter and the nest of dried leaves approx. 50cm below the entrance.

There was no apparent shortage of hollow limbs and termite-ravaged trunks in the woodland habitat occupied by *P. gracilis* and while individual gliders showed preference for certain dens they regularly moved nests and used a variety of widely separated dens through their home range (Figs 16-19), e.g. in the period 10-20 May 1991, adult female T4026 used the 'favoured' nest (nest site 3 of Table 4) on 4 of those days and 7 different dens on the seven remaining days. This female was recorded using a total of 10 different dens.

In addition, gliders familiarised themselves with the mature trees of their home range and spent considerable time exploring hollows and holes in trees other than those known to contain dens. In one case, on consecutive nights, female T4026 descended to investigate a large, long, burnt-out log lying on the forest floor. On both

nights the end of the log was entered at ground level and the glider crawled inside to finally peer out a ground-level pophole for approx 30min before returning to the trees. (On investigation, the inside of the log was found to contain crumbled charcoal, soil and remains of goanna skin, some *Echidna* quills and some patches of pungently smelling possum fur (? *Dactylopsila trivirgata*).

Nests in dens consisted of a thick mat of eucalypt leaves. Animals were not observed collecting or carrying these.

VOCALISATION

Petaurus gracilis was quiet and difficult to locate by calls. The most commonly heard call was a deep, nasal, coarse grunt 'na-when, na-when'. It was not always possible to determine the sex of animals making this call, but those that were sexed were males. The call was sometimes made in response to the play-back defense gurgle ('urga-urga-urga', common to other *Petaurids*) of another individual (see Van Dyck, 1992b). It was also made in response to a human imitation of the 'na-when' call, and imitation was used to survey potential glider sites. One male was heard monotonously repeating this call. This individual was located 3m above ground, pressed head down against the trunk of a *Pandanus citraceus* and in its manner resembled a calling *P. breviceps*. This call was often shortened to a single nasal grunt 'hoy', and often appended by a low 'urga' or two. One sub-adult female once made the simple grunt 'arrgh' on detecting an adult female in a tree nearby. Animals unsure of their security (when exploring unfamiliar territory or when being handled) uttered a soft 'tock-tock'. Calls associated with consorting have been described under 'Reproduction'. Nestling young reunited with their mother after brief separation made a soft 'tzzz-tzzz' call on contact with the female.

DIET

The diet was assessed by directly observing gliders feeding or by analysis of faeces from captured individuals. The feeding observations described below are summarised in Table 6. See Van Dyck (1992b) for further discussion.

Nectar and pollen: Gliders were observed licking nectar (and presumably pollen) from the flowers of a range of trees and shrub species (Table 6). Five faecal pellets were collected during 4 months in 1991 and analysed for food items (Table 7). The pollen assemblage in February was entirely of Myrtaceae pollen, most of which was

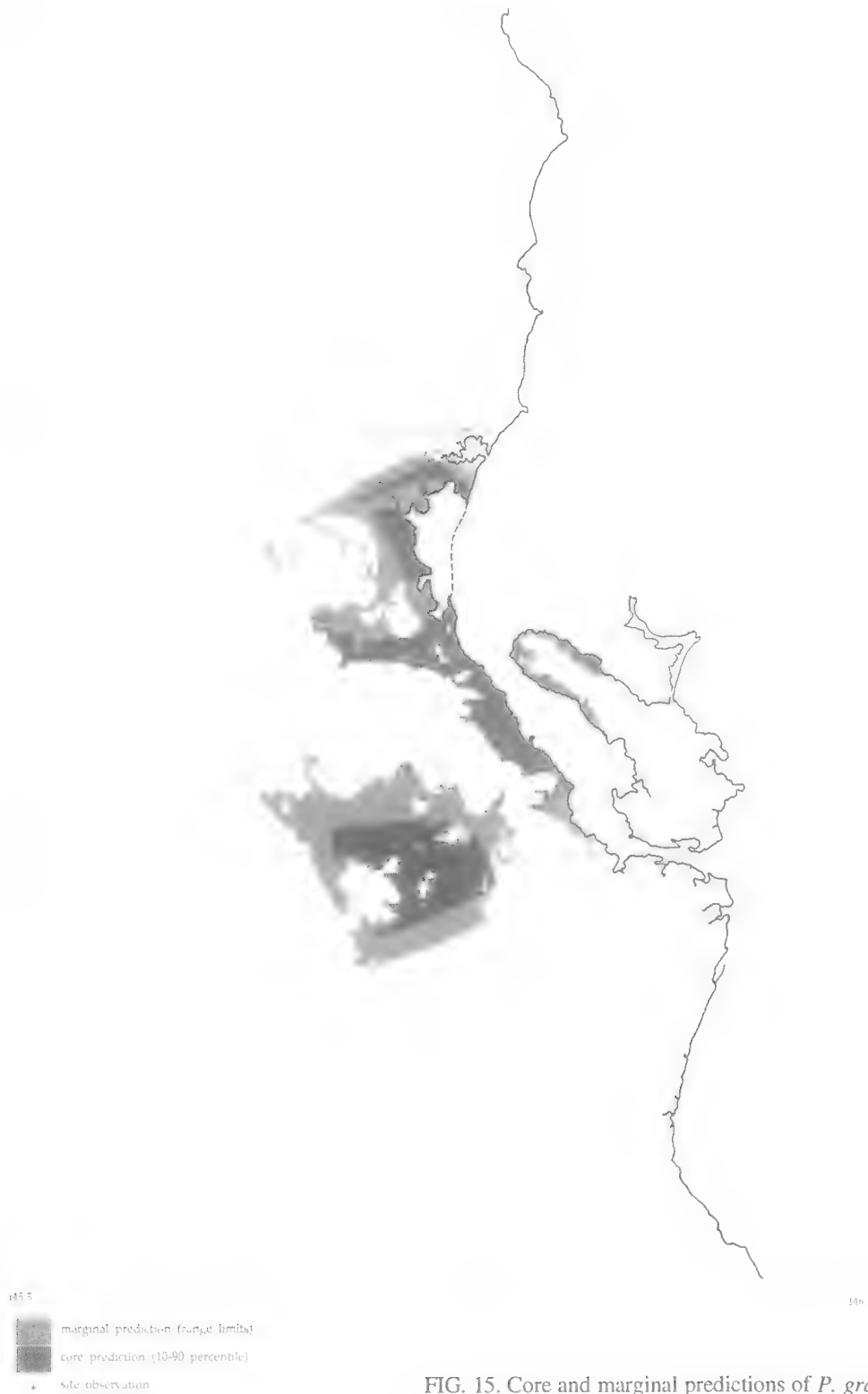


FIG. 15. Core and marginal predictions of *P. gracilis* distribution generated by the BIOCLIM prediction system. (Dotted line shows actual profile of coast).

af4026 (N=101)

Isopleth Areas		Max = 44.59 ha.	
% ha. (%max)		% ha. (%max)	
95 23.01 (51.61)		55 2.20 (5.64)	
90 15.36 (34.44)		50 2.02 (4.54)	
85 9.48 (21.26)		45 1.56 (3.49)	
80 8.39 (18.81)		40 1.20 (2.70)	
75 6.33 (14.19)		35 0.94 (2.13)	
70 4.52 (10.13)		30 0.60 (1.35)	
65 3.33 (7.47)		25 0.37 (0.83)	
60 3.43 (7.69)		20 0.39 (0.87)	

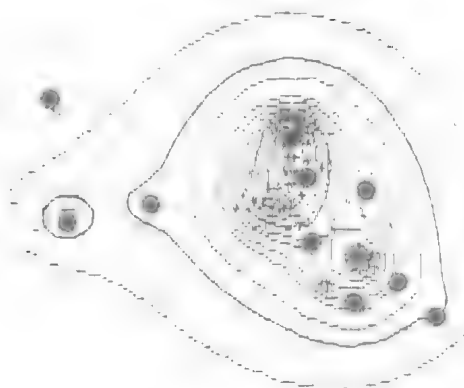
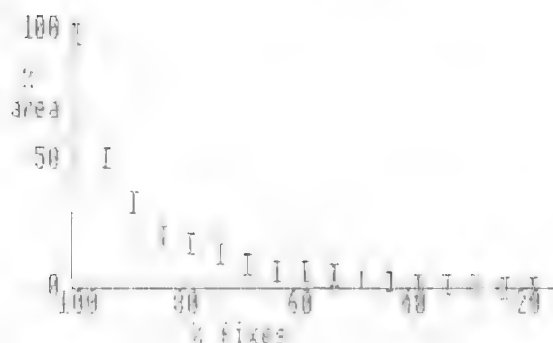


FIG. 16. Harmonic Mean Measure of home range and analysis for adult female T4026. Hard line is drawn over the 95% isopleth. Dots indicate dens used.

comparable to that of *Eucalyptus*. In May, plant material dominated the sample, but pollen was represented in low proportions; also represented were rhomboids of silica. The pollen assemblage contained approximately equal proportions of pollen of *Banksia* and *Xanthorrhoea*. *Banksia integrifolia aquilina*, the only species of banksia recorded at Barretts Lagoon occurred very rarely at the study site.

One female glider was noted eating flower tassels of *Acacia crassicarpa* (each approx. 40mm long: 1 on 12 May 1991, 6-8 on 16 May 1991). Since this wattle produces no discernable nectar it was concluded that such ingestion constituted deliberate pollen feeding.

Xanthorrhoea johnsonii: Two radio-tagged female gliders (T4027, T4028) were observed over extended periods feeding on *X. johnsonii* during May 1991 when flowering was heavy (Table 6). Evidence of scape visitation ('scape' is used for the woody spear-like stalk of the *Xanthorrhoea* fruiting body) at other sites through footprinted scapes (see Fig. 23 and Van Dyck, 1992b) and scape damage, suggested that many other *P. gracilis* visited *X. johnsonii* (e.g. % green scapes footprinted at Nest Site (NS) 1 (see Table

4): 22%; NS2: 25%, NS3: 26%; NS4: 63%). The gliders' process of appraisal of the condition of scapes of *X. johnsonii* was conducted mostly at heights of less than 3m above the ground. Scapes were reached by leaps between thin saplings, small shrubs, dead sticks or other scapes. After landing on a scape, a glider would face downward, descend to within 30cm of the base, then turn and climb quickly up the spear. To reach more isolated scapes gliders crossed open ground in a series of rabbit-like hops through long grass. Fresh spikes ('spike' is used for the flowering head of the *Xanthorrhoea* fruiting body) were glided onto directly, but dried, seeded spikes were not, and although scapes of the previous season were climbed and investigated, the appraisal was abandoned usually within 30-60cm of the spike.

Young scapes with unformed spikes were chewed at the spike base and also at the scape base (Fig. 24) among the leaf insertions, and any amber-coloured mucilaginous exudate from earlier gougings licked off and eaten. *Xanthorrhoea* evaluation by *P. gracilis* occurred in frenetic bouts which ran for as long as 2.5hrs and covered linear distances of up to 800m. Suitable flowering heads were licked thoroughly for nectar (Fig. 25).

saf4028 (N=24)

Isopleth Areas	Max = 19.36 ha.
% ha. (%max)	% ha. (%max)
95 13.86 (71.60)	55 1.53 (7.91)
90 9.66 (49.91)	50 1.53 (7.91)
85 4.23 (21.83)	45 0.36 (1.85)
80 4.23 (21.83)	40 0.36 (1.85)
75 1.71 (8.85)	35 0.36 (1.85)
70 1.53 (7.91)	30 0.36 (1.85)
65 1.53 (7.91)	25 0.36 (1.85)
60 1.53 (7.91)	20 0.36 (1.85)

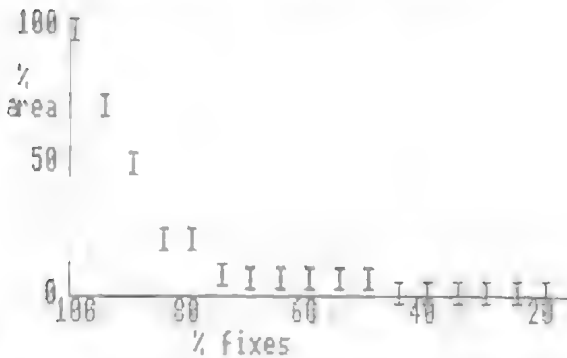
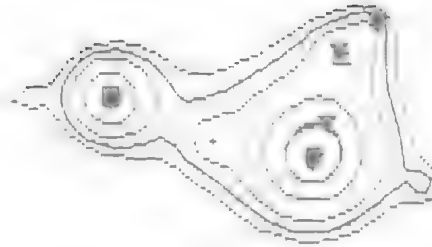


FIG. 17. Harmonic Mean Measure of home range and analysis for subadult female T4028. Hard line is drawn over the 95% isopleth. Dot indicates den used serially with adult female T4026. Triangles indicate other dens used.

One instance of eating unopened flowers was noted.

By August 1991 most *X. johnsonii* flowers had seeded (e.g. NS 1: 80%; NS 2: 50%; NS 3: 58%; NS 4: 62%) and experimental cuts which I made (5 Aug 1991) on immature scapes had produced no exudate up to 5 days after cutting. Although nectar-producing flowers occurred in the study area and pollen was abundant in one of two faecal samples taken (6, 9 Aug) (Table 7), none of the three gliders tracked during this period were recorded feeding on them. Hall (1956) demonstrated significant changes in spike component analysis from preflowering through to flowering. These included drops in protein (11.1% to 6.8%), carbohydrate (63.7% to 45.9%), fat (2.2% to 1.2%), phosphate (0.47% to 0.31%) and an increase in fibre (19.0% to 42.7%) as the spike matured.

Preliminary analysis results of dried gum exudate scraped from *X. johnsonii* scapes in Aug 1991 were as follows: moisture= 25.6%, protein ($N \times 6.25$)=2.5%. Infra-red spectroscopy showed that the substance was a complex mixture consisting of polymerised and/or unpolymerised higher

alcohols and acids. Some carbohydrates in free or bound form were probably also present, but no simple sugars were detected (N. Douglas, pers. comm.). No analysis was made of May *Xanthorrhoea* exudate.

Eucalyptus intermedia and *E. pellita* sap and/or kino: Gliders were often observed feeding at wound sites on *E. intermedia* (Table 6). Here they would pick crusts of dried exudate and lick the surface from which the crust had been taken. The wound was often accompanied by fresh red dribblings of kino which may have been ingested also.

One female glider (T4026) was observed licking and stripping fresh and old longitudinal incisions in the canopy branchlets of *E. intermedia* and *E. pellita* (Table 6). From the *E. intermedia* canopy the process was difficult to observe clearly, but large lumps of hard exudate falling from the glider's mouth were collected on the ground. The process was observed between 2050hrs 11 Aug 1991 and 0327hrs 12 Aug 1991 and involved alternating bouts of licking-biting and motionless rest with mouth away from the wound and eyes often closed (10min feeding, 1hr



FIG. 18. Harmonic Mean Measure of home range and analysis for sub-adult female T4027. Hard line is drawn over the 95% isopleth. Triangle indicates den used conjointly with sub-adult female T4028. Squares indicate other dens used.

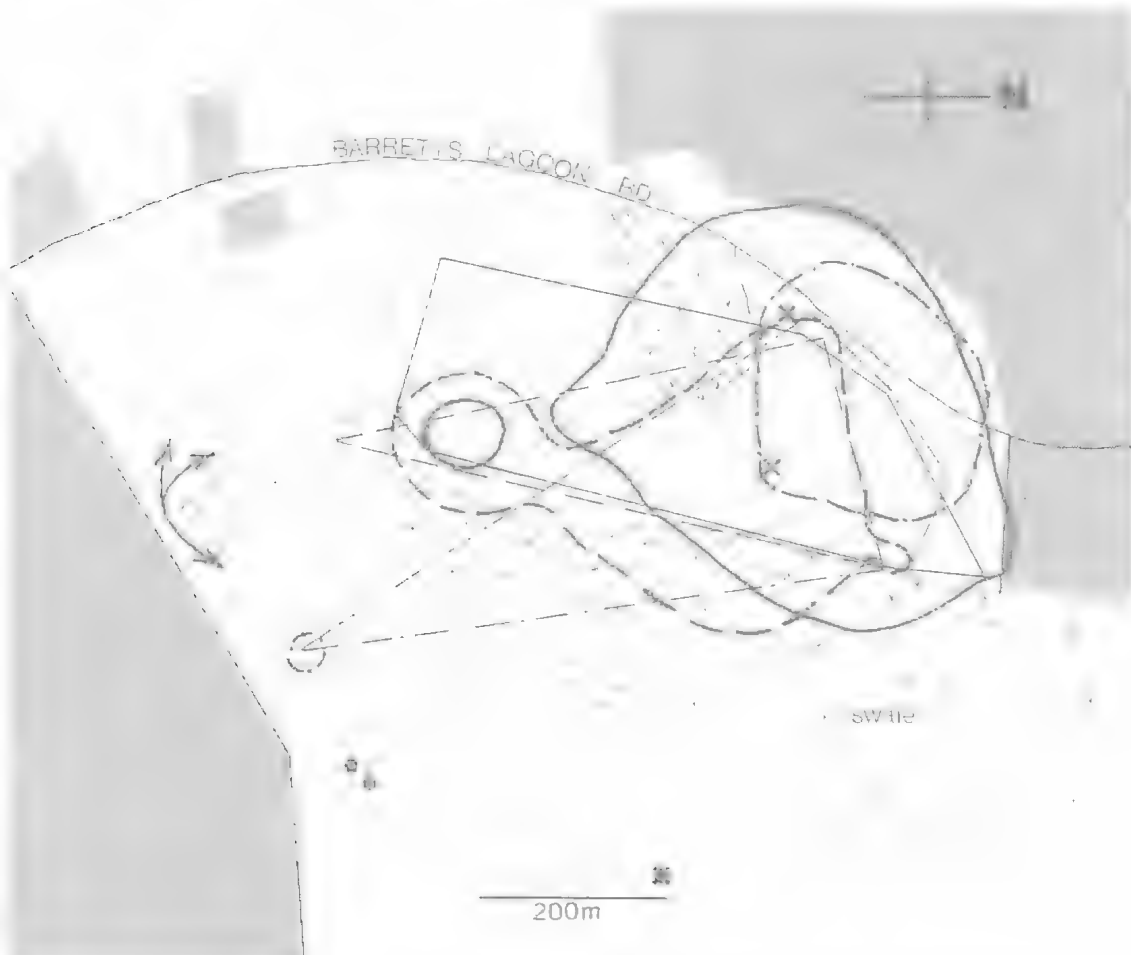
25min resting, 6min feeding, 28min resting, 7min feeding, 16min rest, 9min feeding, 5min rest. Total time feeding in *E. intermedia* 57min; total time resting 2hrs 27min. For *E. pellita* total time feeding 29min; resting 36min). Branchlets retrieved the following day from the feeding sites (approx. 17m high in the *E. intermedia* and approx. 8m in the *E. pellita*) showed many incisions of varying size and state of repair on thin branches that ranged from 4.7mm to 14mm in diameter (Fig. 26). For the *E. intermedia* sample (diameter 4.7- 12.9mm), incised cut lengths varied from 9.2-87.6mm (mean length= 46.4mm, N=16 from 9 branchlets all less than 40cm long) and cut width varied from 1.3-3.9mm (mean width: 3.2mm). For the *E. pellita* sample (diameter 10.1-14.00mm) incised cut lengths varied from 59.6-133.00mm (mean length= 91.5, N= 6 from 4 branchlets all less than 40cm long) and cut width varied from 2.0-7.6mm (mean width 3.3mm). Cuts from both species of eucalypt had healed and calloused leaving a raised 'lip'-like ridge around a ribbon of exposed sapwood. Cicadas had oviposited in the sapwood of most of these cuts (exposed sapwood of all long incisions (i.e. 9 >50mm) in the *E. intermedia* sample and of 4 in

the *E. pellita* sample). The fresh *E. intermedia* incision sites carried red kino stain on and under the calloused edges of the incision, but this was not as apparent in the *E. pellita* incisions.

A sample of bloodwood kino was taken from the branches showing fresh incisions. Preliminary analysis results were as follows: moisture 39.6%, protein (N \times 6.25) 1.3%. Infra-red spectroscopy showed the substance was a complex mixture consisting of polymerised and/or unpolymerised higher alcohols, probably containing carbohydrate material either in bound or free form. It was not possible to characterise these components more precisely, or to determine the proportion of apparent carbohydrate in the exudate. However no simple sugars were present in free form (N. Douglas, pers. comm.).

Although not visible from the ground, wounds similar to those described above are very common in the small branches of the canopy in *E. intermedia*, *E. pellita* and *E. clarksoniana* throughout the range of *P. gracilis*. As yet there are no criteria for distinguishing cuts made by *P. gracilis* from those of *P. breviceps*, which occurs sympatrically with *P. gracilis* but is not tolerated socially by it.

FIG. 19. Overlap in home ranges of adult female T4026 (—), sub-adult female T4027 (---) and sub-adult female T4028 (— · —). The MCP boundaries are represented by thin lines corresponding in pattern with the respective 95% isopleth indicated by the thick, curved lines. Crosses indicate the location of the 3 dens used by adult male T4030 over 3 consecutive nights (7-9 Sept 1991). Dots indicate the only 3 dens used by adult female T4031 during the period 9-15 Sept 1991. Arrows indicate the only natural corridor connecting land north and south of the central swale. Shaded areas indicate cleared land.



Acacia arils and gum: One female (T4026) was observed on 27 Nov 1991 from 1742 hrs to 0330 hrs (28 Nov 91) (Table 6). During that time the glider, which had fully furred young in the nest, fed almost exclusively on arils of *A. crassicarpa* (Fig. 27) which it collected from gaping pods. The only other food eaten during the night was a grasshopper/katydid caught by the glider while in the process of aril feeding. Gum exudates of *A. crassicarpa* were licked and new sites on a trunk were roughly gouged and torn open.

Lichens: A female (T4026) was observed 16 Aug 1991 from 0200hrs-0230hrs feeding on lichen growing on the bark of *Lophostemon*

suaveolens. The glider chipped off flakes of bark, licked the lichens off then let the bark chip fall. A sample of lichen taken from the feeding site contained only clonal reproducing bodies (soredia) and was unidentifiable (R. Rogers, pers. comm.).

Psyllids and honey dew: A female (T4026) was observed on 13 Aug 1992 from 2000-2130hrs feeding on the psyllid *Eriococcus* sp. (Fig. 28) which had infested the underside of leaves in the canopy (at 10m) of an *E. pellita* (Table 6). The glider appeared to scrape and lick psyllids off the leaves' mid-vein. Results of preliminary analysis of scale insects are as follows: moisture= 55%, lipids= 13.2%, protein ($N \times 6.25$)= 20%. Of the



FIG. 20. Nestling young of female T4026 (T4032 and T4033) photographed 26 Nov 1991.

13.2% lipids in the sample, 6.3% could be regarded as higher molecular weight glyceride waxes and the remaining 6.9% as fatty oils. The protein figure was obtained by applying the conversion factor normally used for converting nitrogen content to protein, however nitrogen would be present not only in the protein but also in the chitin. The analysis was not able to differentiate between nitrogen derived from protein and that contained in chitin (N. Douglas, pers. comm.).

A male was observed on 2 Oct 1992 licking along the underside of *E. intermedia* leaves. It appeared to consume both the psyllid *Eucalypstolyma distincta* and its lerp (Fig. 29).

A female (T4026) was observed 13 Aug 1991 licking honey dew off the upper and lower surfaces of leaves of *E. pellita*.

Other arthropods and arachnids: Large insects were usually manipulated and consumed while the glider hung upside-down by the hind legs against a tree trunk, leaving the forelimbs free to manipulate prey. In the case of a large grasshopper, the gut was dismembered and extracted by biting and holding one end of the insect in the mouth, holding the other end in the forefeet, extending the forelimbs fully, tossing the head back and thereby stretching out the gut in a long string. A female (T4026) was once observed catching a flying moth by grabbing it with the forefeet alone.

On 13 Aug 1991, a female glider (T4026) was observed tearing into an occupied arboreal nest of

Green Tree Ants and for 5 minutes after, eating something taken from the nest. The act of breaching the nest was undertaken at some apparent discomfort to the glider which shook its legs and flicked ants off its body for the following 20 minutes.

The stomach of an adult male glider collected on 9 Dec 1989 while feeding in flowering *E. tessellaris* contained the remains of numerous scarabaeid beetles which, presumably, had also been feeding at the flowers.

Water: After rain, gliders were observed licking water off petioles and leaves of *L. suaveolens* and *E. intermedia*. During rain, one glider was observed to move under the protective cover of a thick semi-horizontal branch. It remained still with head down until the rain passed. This animal dried its wet tail by thrashing it from side to side.

DISCUSSION

TAXONOMY

Alexander (1981) commented that, of the recognised subspecies of *P. norfolcensis* and *P. breviceps*, *P. n. gracilis* and *P. b. longicaudatus* needed further detailed revision before they could be accepted as valid races. He noted that *P. n. gracilis* was based on one specimen from north of Cardwell, differing from the nominate subspecies in its markings, shorter ears, and a more slender tail; all features he demonstrated to be highly variable in specimens of *P. norfolcensis* from Queensland to Victoria. Had de Vis drawn attention to only those features, it could have been said that he described *P. gracilis* for all the wrong reasons. But de Vis also made a note that 'In size [*P. gracilis* was] intermediate between *B. australis* and *B. sciureus* [*P. norfolcensis*]' (de Vis, 1883: 620), a significant statement that has not received the attention due to it in the literature. The set of measurements which accompany the de Vis description lie well outside those given by Thomas (1888) for specimens of *P. norfolcensis*. The lowland Tully-Ingham gliders I have attributed to *P. gracilis* are, in size, consistent with the large dimensions outlined in the de Vis description and, by the veracity they impart to the original measurements, reinforce the suspicion that neither Thomas nor subsequent authors who also dealt with *P. gracilis* as a synonym of *P. norfolcensis* had ever made a personal examination of either the specimen de Vis described in 1883, or of any other similar glider from nearby.

In body and tail length *P. gracilis* is similar to the large New Guinean glider *P. abidi* (Fig. 5).



FIG. 21. *Eucalyptus intermedia* nest tree (Nest Site 1 of Table 4) showing entrance hole (top arrow) 3m above nest (bottom arrow).

However, dental and biochemical systematic studies (Van Dyck, 1990; Colgan & Flannery, 1992) put *P. gracilis* closest to *P. norfolcensis*. The dental morphology of *P. abidi*, in particular the unreduced nature of P^2 , the unreduced protocone of M^2 , and the broad ectoloph of M^2 and M^3 suggest a more pleisomorphic species from which the Australian species *P. gracilis*, *P. norfolcensis* and *P. breviceps* could have been derived.

The large size of *P. gracilis* is worth noting in the context of its close affinities with *P. norfolcensis*. Alexander (1981) concluded that Victorian populations of *P. norfolcensis* were significantly larger than those of southeast Queensland, and that the size increase from north to south was gradual and continuous, thereby representing a latitudinal clinal variation in body size which could be attributed to Bergmann's rule. All adult specimens of *P. gracilis* examined (from latitudes $18^{\circ}02'$ – $18^{\circ}27'$) were larger in skull length (maxskull length: mean = 51.14, N =

7, SD = 0.95) than Victorian *P. norfolcensis* (mean = 47.52, N = 5, SD = 0.64) from latitudes $36^{\circ}23'$ – $38^{\circ}26'$, and significantly larger ($P < 0.001$) in body length than Victorian *P. norfolcensis* (for *P. gracilis* mean = 247.45, N = 11, SD = 15.86; for *P. norfolcensis* mean = 212.40, N = 5, SD = 16.69). This reversal in the clinal trend in *P. gracilis* is offset by normal trends attributable to Bergmann's rule seen in other possums and gliders such as *P. breviceps* (Smith, 1973), *P. australis* (Russell, 1984), *Petauroides volans* and *Trichosurus vulpecula* (Yom-Tov & Nix, 1986).

FOOD SELECTION

It is as difficult to account for the selective pressures resulting in large body size in *P. gracilis*, as it is to interpret the 'impetus for body size development' (Smith & Lee, 1984) in the entire Petauridae given the minor dietary differences between the species. Among exudivores *P. gracilis* is more of a dietary opportunist, feeding on nectar, pollen, arthropods, arachnids, wattle exudates, honeydew and eucalypt saps when these food items become seasonally available. Although similar diets have been thoroughly documented for other petaurids such as *P. breviceps* (Fleay, 1947; Smith, 1980, 1982; Suckling, 1980; Suckling & McFarlane, 1983) and *P. australis* (Smith & Russell, 1982; Henry & Craig, 1984; Craig, 1985; Goldingay, 1986, 1987; Kavanagh, 1987a, 1987b) the occurrence of other significant dietary items such as *Acacia* arils, *Xanthorrhoea* exudates, *E. intermedia* sap and/or kino, lichens and green tree ants (or the contents of their nests) has not been reported for the group.

Australian *Acacia* species have been divided into three dispersal groups (O'Dowd & Gill, 1986): 1, arillate *Acacia* that are bird dispersed (17% of 92 species sampled), 2, arillate *Acacia* that are ant dispersed (74%); and 3, the remaining non-arillate *Acacia* species (9%) that do not correlate with dispersal by ants or birds. O'Dowd & Gill showed that in bird-syndrome species diaspores (dispersal units) were as follows: predominately bicoloured, displayed in dehiscent pods retained in the canopy, high in aril mass and lipid content and significantly longer and more contorted than in ant dispersed *Acacia*. Diaspores of ant-syndrome species were presented inconspicuously on the ground and investment was low.

In the broad sense, bird and ant dispersed seeds are thought to escape from interspecific competition, fire, parental competition and seed predators, and/or benefit from transportation to



FIG. 22. *Lophostemon suaveolens* nest tree (Nest Site 3 of Table 4) showing relative size of entrance hole.

microsites with superior nutrients (Holldobler & Wilson, 1990). O'Dowd & Gill (1986) considered two of these most relevant to the *Acacia* group: escape from the detrimental effects associated with the parent plant, and an increased chance of being directed to specific microhabitats by the dispersal agent. They note that in some *Acacia* species, lipids might account for 70% of the aril dry mass, a value comparable to the highest lipid contents observed in seeds and fruits. They argue that lipids provide a greater energy reward per unit mass of aril, since lipids yield roughly twice the energy upon catabolism as carbohydrates, and they conclude that since most of the known dispersal agents of *Acacia* are generalist feeders and incorporate insects into their diet, the higher proportion of saturated fatty acids may 'mimic' the saturated fatty acid composition typically found in animal prey.

Petaurus gracilis stands to gain much from the summer aril harvest provided by *A. crassicarpa*,

a bird-syndrome *Acacia* whose arils, though not brightly coloured, are long (convoluted around 14mm) and prominently displayed (Fig. 27) in the canopy over many weeks. Female gliders in late lactation (December) with nestling young in dens surrounded by seeding *A. crassicarpa* might be expected to significantly reduce energy costs by foraging on arils close to the nursery den. As the gliders did not eat the *Acacia* seeds, but discarded them below the tree, it is doubtful that the tree derives anything advantageous from the relationship.

The August 1991 observation of a glider breaching an occupied arboreal nest of Green Tree Ants and for 5 minutes thereafter eating something taken from the nest, deserves comment here. Larvae were initially considered the objects of the glider's attention. However, nests breached by M. Hopkins (pers. comm.) in an



FIG. 23. New scapes of *Xanthorrhoea johnsonii* carry a 'bloom' of waxy spicules. Gliders visiting scapes leave long-lasting footprints in the wax. Surveys of *P. gracilis* habitat are facilitated by an inspection of *Xanthorrhoea* inflorescences.



FIG. 24. *Xanthorrhoea johnsonii* scape showing tapping gouges attributed to *P. gracilis*.

unrelated study, were found to contain abundant harvested *Acacia* arils. Three *Acacia* species occur commonly in *P. gracilis* habitat: *A. crassicaarpa*, *A. flavescens* and *A. mangium*. However the three species flower concurrently through May making it unlikely that mature arils would be available for harvest and storage as early as mid-August. Given the longevity of arils it is possible that the items extracted from the nest were arils harvested by the ants the previous summer.

The grasstree *Xanthorrhoea johnsonii* has a wide geographic and environmental range on the east coast, tablelands and western slopes from Cape York Peninsula south to Singleton, New South Wales (Bedford et al., 1986). Unlike most other glider sites within the surveyed area, *X. johnsonii* was common at Barretts Lagoon with densities exceeding 1000 plants per 1000m². There, soils were waterlogged for extended periods during the wet season, and flowering in both 1991 (a non-fire year) and 1992 (severe fire in

early January) occurred from May to August. During this time both *P. gracilis* and *P. breviceps* were observed feeding (separately) on spike nectar, but only *P. gracilis* was observed tapping young scapes for exudate (Van Dyck, 1992b). As scapes and spikes matured it became difficult to distinguish between scape damage due to gliders and that caused by insects. Large crickets were noted grazing broad (5mm) shallow channels in immature upper scapes which later oozed exudate and calloused to leave scars similar to those left by gliders. As scapes further matured, a glider's bite at the base of a scape could have been interpreted as either a gum tap or an attempt to get at worm-like beetle larvae that sometimes excavated burrow networks in the lower part of the scape.

Pollen analysis showed *Xanthorrhoea* pollen intake between May and August and rhomboidal crystals of silica in the May 10 sample. The presence of the silica crystals demonstrates that



FIG. 25. *Xanthorrhoea johnsonii* spike being licked by sub-adult female *P. gracilis* T4027.

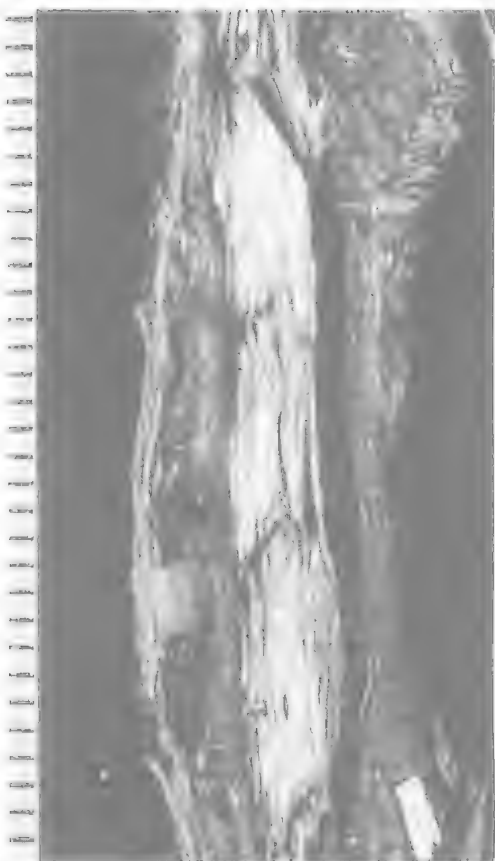


FIG. 26. Branch of *Eucalyptus intermedia* stripped for sap and/or kino by *P. gracilis*. Note cicada ovipositions.

the glider may have foraged scape tissue of *Xanthorrhoea*, as rhomboidal silica surrounds the secondary bundles of this taxon (Staff & Waterhouse, 1982). In May, a high proportion of scapes were tender and, presumably most productive when tapped. The results also suggest a high percentage (up to 70%) of *Xanthorrhoea* pollen is available for digestion through release of the contents via the aperture. *Xanthorrhoea* pollen may provide a convenient and rich source of protein by virtue of the high ratio of pollen aperture to surface area making the contents more readily available than pollen from other sources e.g. *Eucalyptus* (M. Dettmann, pers. comm.). Pollen has a high protein content (6-34%, Smith, 1982). Given the carbohydrate and protein rewards offered by *X. johnsonii* over a long period, the intake of scape exudate is noteworthy in respect of its possible digestibility-reducing or toxic secondary plant compounds. Investigations of the complex mixture of aromatic compounds

found in *Xanthorrhoea* have concentrated on resins present in the trunk (Birch & Hextall, 1955; Duewell 1955, 1965, 1968; Duewell & Haig 1968) but not in the scape. Phenols and flavinoids are known components of young scapes (D. Bedford, pers. comm.) and their injection by cattle has been attributed to poisonings during autumn and early winter in north Queensland (the sometimes fatal condition known as 'wamps' or 'crampy disease'). The toxic principle involved in such poisonings has not been investigated (Everist, 1974). Hall (1956, 1965) noted that young *Xanthorrhoea* spikes (probably *X. fulva*, D. Bedford, pers. comm.) appeared to be more toxic than old ones, and there was evidence to suggest that the scape was more poisonous than the spike.

Australian folivorous marsupials have been shown to exhibit a number of physiological and morphological adaptations to cope with xenobiotic compounds such as tannins and other polyphenols in their diets (Hume et al., 1984; Foley, 1987; Foley & Hume, 1987; Foley et al., 1987). The development of the hindgut, in particular the caecum, into a fermenting chamber, is



FIG. 27. Prominently displayed seeds and arils of the 'bird-syndrome' *Acacia crassicarpa*. This *Acacia* is an important understorey component of *P. gracilis* habitat.

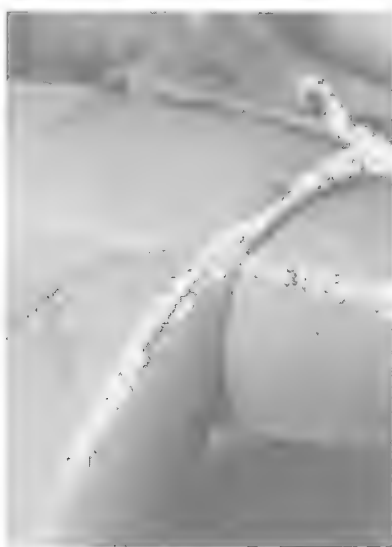


FIG. 28. *Eriococcus* sp. on *Eucalyptus pellita* foliage. Both scale and psyllid are eaten by *P. gracilis*.

one of these adaptations and its role in the bacterial fermentation of carbohydrate polymers (some plant gums) eaten by petaurids is discussed by Smith (1982a, 1982b). In external proportions, the alimentary tract of *P. gracilis* (Fig. 30) resembles that of *P. breviceps*. In one specimen of *P. gracilis* (JM7400), the small intestine (44cm) tapered gradually from 1.3cm diameter below the duodenum to 2.9cm diameter at the point of junction with the hindgut and caecum. The caecum was 7.8cm long and broadest at 1.5cm. The colon was long (25cm). The length of the caecum in *P. gracilis* was roughly twice that (or 11.3% of total gut length) of the caecum in the striped possum *Dactylopsila trivirgata* (6.9% of total gut length, see Smith, 1982b). The colon in *P. gracilis* occupied approximately 36% of total gut length and compared to 17.2% in *D. trivirgata*. The striped possum has a similar body weight to, and occurs sympatrically with, *P. gracilis* through most of the latter's range. If this difference in the capacity of the hindgut reflects a physiological advantage in *P. gracilis* to deal more successfully with the toxic polyphenols and complex carbohydrates of *Xanthorrhoea* gums and exudates, it may provide further ecological segregation between the two species.

This segregation may further be reinforced by the ability of *P. gracilis* to deal with lichens whose secondary chemicals (toxic polyphenols) may be a defense response to predation or an aggressive allelopathic response (Lawrey, 1986;

Rogers, 1990) and Pink Bloodwood (*E. intermedia*) sap and/or kino (although precisely which one of these or what proportions the glider takes from branchlet slashings and small trunk wounds is not known). Old, red-stained, calloused slashings were often found to be fed by kino ducts, and did not display crusted kino on the wound, suggesting that either this type of wound may not crust over naturally, or gliders may have cleared away or eaten the crystalline form and then fed on kino liquor as it leaked into the wound. Kino, the 'blood' from which the group of 'bloodwood' eucalypts are renowned and named, is astringent to taste and contains large quantities of toxic polyphenols (Smith, 1982). The results of chemical analysis of Pink Bloodwood kino from Barretts Lagoon suggested broad superficial similarities to *Xanthorrhoea* exudate. Gliders of any species have not previously been reported to feed on kino.

Phloem sap feeding is well documented for *P.*



FIG. 29. *Eucalyptolyma distincta* on *Eucalyptus intermedia* foliage. Both lerp and psyllid are eaten by *P. gracilis*.



FIG. 30. Dissected gut of *P. gracilis* (JM7400).

breviceps and *P. australis* (see previous references). Smith (1982) noted that when gliders fed on sap they were generally seen to chew the sides of the wound and Craig (1985) described bark stripping in *P. australis* where bark and adhering conducting tissues of both *E. cytellocarpa* and *E. obliqua* were stripped to a depth of 1-2mm and torn free in long slivers, which were immediately discarded and the damaged surface licked intensively. It is possible that similar gouging behaviour observed in *P. gracilis* in the canopies of both *E. intermedia* and *E. pellita* was directed at phloem sap and not at kino. In that no actively

worked sap-site trunks such as those characteristic of *P. australis* were detected over the course of the survey, it may be that for *E. intermedia* at least, thin canopy branches provide the most convenient access to phloem sap where trunk gouging might be too quickly counteracted by a kino injury response. Given the critical importance of the northern bloodwood complex (*E. intermedia*, *E. clarksoniana*, *E. dolichocarpa*) to the distribution of *P. gracilis* (see below), the shortcomings associated with knowledge of this glider's relationship with these species need to be addressed. Given its relatively large size, *P. gracilis* may be dependent on this group for incising and thereby the geographic range of the glider is, in part, determined by the presence of these trees.

DISTRIBUTION AND HABITAT

Sites supporting *P. gracilis* are characterised by very high (seasonal) precipitation and a woodland vegetation blend that is shaped and maintained by fire. The glider's narrow range coincides with the wettest zone in Australia (Tully's mean yearly total rainfall is 4188mm). Coastal areas at the southern limit of the *P. gracilis* range may appear suitable in habitat (e.g. Clemant State Forest 34, near Rollingstone) yet fail to support petaurids other than *P. breviceps*. Large, mature woodland trees of the coastal ridges and plains (e.g. *E. intermedia*, *E. pellita*, *L. suaveolens*) are shallow-rooted, and although trees in such low-lying areas are subject to protracted periods of seasonal inundation, their sandy soils also drain quickly and thoroughly during the extended winter-spring dry season. It is most likely that the ultimate climatic parameter determining the distribution of *P. gracilis* is a dry season moisture threshold (probably close to 100mm dry quarter precipitation) below which its moisture demands cannot be easily satisfied.

Ironically, the high rainfall requirement which partly determines the glider's presence in an area also potentially undermines its long-term survival prospects. Many dryland communities suitable to *P. gracilis* are actively evolving from sclerophyll to vine forest because of changing fire regimes (P. Stanton pers. comm.). Traditional burning practices no longer operate in the area and the threat of economic loss through damage to sugarcane and pine plantations acts as a discouragement to burning-off in adjoining woodland areas. This is linked to a public perception that fires are a 'bad' thing and rainforests are 'best'. Rapidly evolving rainforest communities

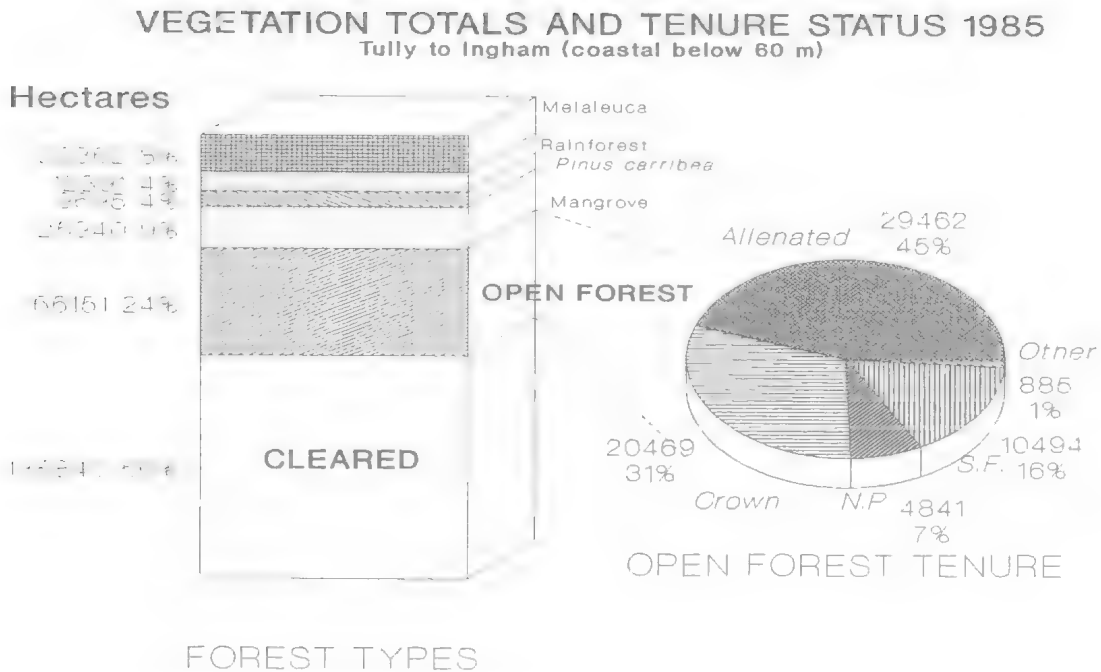


FIG. 31. The status of vegetation types (in general) and open forest (in particular) throughout the range of *P. gracilis*. For coverage see Fig. 1 (Smiths Gap south to Bambaru). Figures supplied by Queensland Forest Service.

were noted in woodlands at the Hull River site, Edmund Kennedy National Park, Murray Upper, Hinchinbrook Is. and parts of Barretts Lagoon.

Petaurus gracilis is dependent on mature stands of mixed-species remnant woodland. The presence of at least one of the 'bloodwood' group (*E. intermedia*, *E. clarksoniana*, *E. dolichocarpa*) and an accompanying species of bird-syndrome *Acacia* (usually *A. crassicaarpa*, less often *A. flavescens* or *A. mangium*) is suggested as a minimal basis for suitable habitat. In a few cases, the place of a bloodwood might be taken by *E. pellita*. This species flowers heavily in February and March, coinciding with bloodwood flowering. Hypanthiums of *E. pellita* blossoms range from 6-10mm, and gliders have been observed to spend entire nights feeding in individual trees (see Goldingay, 1987, 1989 for similar behaviour in *P. australis* at single sap-sites). The presence of *E. pellita* was considered to indicate areas of high quality glider habitat. Where mature *E. pellita* combined with *Xanthorrhoea johnsonii*, the resultant habitat blend could often be regarded as optimal (e.g. areas of Barretts Lagoon). Habitat considered sub-optimal was characterised by a trend

toward species-poor assemblages and dominance by a single eucalypt species e.g. *E. platyphylla* (Wharps Holding), *E. clohesiana* (Hinchinbrook Is.), *E. intermedia* (Graham Range National Park). A curious human bias toward leaving mature *E. tereticornis* in cultivated paddocks and narrow belts along roadsides (e.g. Kennedy Valley, Ashton and Lannercost Creeks) has meant that gliders can often occupy heavily degraded and fragmented habitat where vestiges of suitable riparian (gully) habitat provide summer requirements. *Eucalyptus tereticornis*, a mid-winter flowering species is known as a major source of winter pollen and a useful source of nectar (Penfold & Willis, 1961; Chippendale, 1988). Also the presence of many large mature specimens of *Deplanchea tetraphylla* distributed sparsely but evenly throughout the glider's range is considered important in that they provided an abundant source of nectar (and perhaps pollen) at a time (August, September) when little else is in flower.

SOCIAL ORGANISATION AND HOME RANGE

The small sample size upon which these comments are based should not be ignored. Barretts

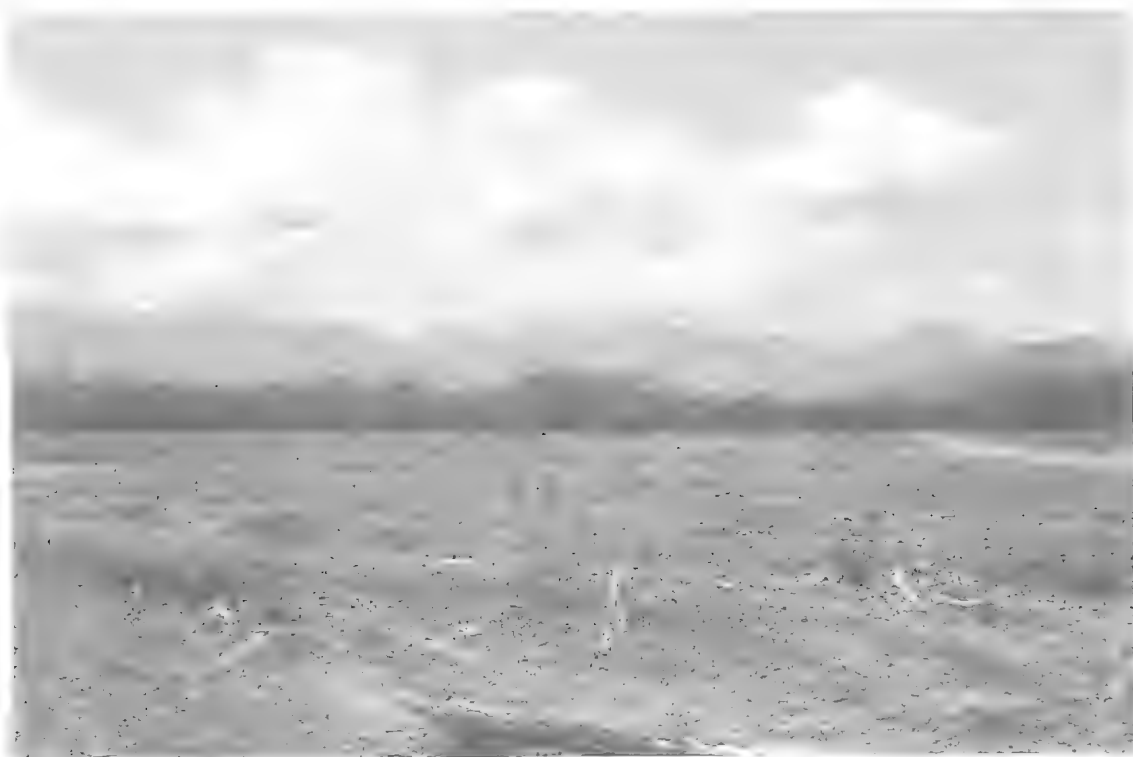


FIG. 32. Lowland woodland clearing for *Pinus caribaea* plantations has accounted for a loss of at least 9,695ha of *P. gracilis* habitat. In late 1992 Queensland Forest Service suspended clearing of native forests near Cardwell following the recording of *P. gracilis* in foothill remnants at Porters Creek (shown here overlooking Hinchinbrook Is.).

Lagoon, where a total of five gliders were radio-tagged, included patches of habitat considered optimal for *P. gracilis*. The woodland community was structurally complex with abundant species of *Eucalyptus* (4), *Melaleuca* (4), *Acacia* (4) and with a dense understorey of *Xanthorrhoea*. The availability of diverse sources of carbohydrate and protein throughout the year (see Table 6), combined with an abundance of nest sites, could be expected to be reflected in a polygynous mating system (Emlen & Oring, 1977; Lee & Cockburn, 1985; Henry, 1984; Goldingay, 1992) as polygyny in the Petauridae is thought to evolve when resources are abundant enough for male gliders to defend a territory which can support more than one female consort. However, *P. gracilis* appears unconventional in its pattern of social organisation. The two adult females in this study had home ranges that appeared to be relatively exclusive of one another (Fig. 19). Two dispersing sub-adult females were largely solitary although their home ranges overlapped consistently with one another and with one of the adult

females (presumed to be their mother). The adult male denned either alone or with either solitary adult female and regularly spent time with at least one of them for part of the night. This system is a departure from the nature of polygynous mating systems generally attributed to either *P. breviceps* (polygynous: Smith, 1980; Suckling, 1980) or *P. australis* (monogamous: Craig, 1985; Goldingay & Kavanagh, 1990; polygynous or monogamous: Russell, 1984; Goldingay, 1992). The apparent system in *P. gracilis* more closely approximates that seen in *Petauroides volans* (Henry, 1984; Kehl & Boorsboom, 1984), although the home range is much larger in *P. gracilis* (23ha for an adult female compared to 1.25–2.5ha in a *P. volans* female), and the investment in female and/or resource defense by male *P. gracilis* could be anticipated to greatly exceed that by male *P. volans*.

It is tempting to draw similarities between the social behaviour of *P. gracilis* and that of the tropical African exudivorous prosimian *Galago senegalensis moholi* as reviewed by Bearder

TABLE 6. Food items recorded for *P. gracilis* by direct observation.

Food item	Source	Month recorded	Locality (from Table 1)
Nectar and pollen	Blossoms of:		
	<i>E. pellita</i>	Feb, Mar	7, 14, 15, 19
	<i>E. clarksoniana</i>	Mar	6, 14
	<i>M. elleryana</i>	Mar	9
	<i>X. johnsonii</i>	May	19
	<i>A. crassicarpa</i>	May	19
	<i>E. tereticornis</i>	Jun	5, 19
	<i>D. tetraphylla</i>	Aug	19
	<i>M. dealbata</i>	Oct	19, 1
	<i>E. tessellaris</i>	Nov	19
Incision exudates	<i>A. crassicarpa</i>	May	19
	<i>X. johnsonii</i>	May	19
	<i>E. intermedia</i>	Sep	19
	<i>E. pellita</i>	Sep	19
Acacia arils	<i>A. crassicarpa</i>	Dec	19
Lichen	<i>L. suaveolens</i>	Aug	19
Spiders/Insects	large (?huntsman) spider	May	19
	cockroach/beetle	May	19
	green ants or nest contents	Sep	19
	moth	Sep	19
	grasshopper/katydid	Dec	19
Psyllids and lerp			
<i>Erriococcus</i> sp.	<i>E. pellita</i>	Aug	19
	<i>E. intermedia</i>	Aug	19
<i>Eucalyptolyma distincta</i>	<i>E. intermedia</i>	Oct	20
Honey dew	<i>E. pellita</i>	Sep	19

(1987). In *G. senegalensis moholi*, female territories are large enough to support feeding throughout the year and in homogeneous habitat, home ranges of females are approximately equal in size. Females signal territory ownership to conspecifics by scent marking and vocalisation; only adult females are repulsed. At first an adult daughter may share her mother's territory, but later there is less overlap although related females may share critical resources (up to 4 adult *P. gracilis* were once recorded feeding simultaneously in a single flowering *E. tessellaris* at Barretts Lagoon). Territories of male *G. senegalensis moholi* (i.e. 'A-males', which are older, heavier

and territorial and have preferential contacts with females) overlap those of one or more females. A-male territories are signalled by scent and vocalisation and other adult males are repulsed. There is no relationship between male territory size and dietary requirements. A special bond of familiarity links a territorial male to his females. This bond is serviced by regular visits that involve direct contact with the females. The direct contact may be prolonged (several hours). Additionally, calling and indirect contact using scent marking may be employed. Male stability and territoriality depends on the presence of females. Male-male and female-female territories (between matriarchies) have zones of overlap where territorial signals are exchanged.

Bearder (1987) notes that such a strategy in *G. senegalensis moholi* ensures the even spacing of single females or matriarchies throughout areas of suitable habitat and ensures that the nature of male territoriality ensures mating access to females without wasting energy on subordinates. Smith & Lee (1984) comment that theoretically, female possums might be expected to obtain more nutrients for survival and reproduction when solitary (and defending solitary territories) except when specific advantages of clumping outweigh the disadvantages of sharing resources. Given the combination of its moderately large size, and the benign tropical climate associated with its habitat, *P. gracilis* could be expected to have a low relative cost of thermoregulation and as a result it may avoid group huddling.

The threat from Rufous Owls (*Ninox rufa*) and Lesser Sooty Owls (*Tyto multipunctata*) which occur commonly throughout the range of *P. gracilis* may also make lone foraging a response to crypsis for defense (Henry, 1984, for this behaviour in *P. volans*). Of 5 regurgitated pellets retrieved from a Rufous Owl's nest site at Lanercost, 1 pellet contained maxillary fragments of an adult specimen of *P. gracilis*.

The Barretts Lagoon situation may reflect an artificial situation in that the adult female home ranges were separated by an extensive treeless swale with one narrow natural corridor connection at the southern end (Fig. 19). The western side of one of those home ranges was bordered by a road. Investments in female resource defense by the male may have thereby been greatly reduced, and elsewhere, in areas of more contiguous habitat, *P. gracilis* may prove to exhibit a mating system compatible with that described for other petaurids.

If the mating system at Barretts Lagoon was

typical, the quasi-polygynous system may offer abundant resources of food and time to reproductive males, yet just sufficient resources for reproductive females to feed themselves, and tolerate two, large, weaned young (and perhaps a second litter) dispersing slowly from the female's home range. The use by females of multiple dens scattered throughout the home range may represent a cost effective method of territory defense. Home range size and mating strategy have been shown to vary in *P. australis* with the productivity of the site (see Goldingay, 1992 for review). It is likely that in marginal to poor habitats (e.g. Wharps Holding), the sociocology of *P. gracilis* will vary from that of Barretts Lagoon.

CONSERVATION STATUS

Most records of *P. gracilis* (Table 1) have come from altitudes below the 60m contour (mean altitude = 17m; SD = 19.8; SE = 0.35; N = 57). The total area encompassing site records to date of *P. gracilis* is shown in Fig. 31. Of this total area which amounts to 438,454ha, approx. 63% (275,379ha) occurs below the 60m contour. Of this lowland vegetation approx. 50.4% (138,840 ha) has been totally cleared of forest through primary production (mainly establishment of sugar-cane, cattle, bananas, pineapples, fruit trees, aquaculture), logging, and the cultivation of *Pinus caribaea* in plantations (9,695 ha) since 1967. The balance of open forest which totals approx. 66,151ha and represents a surviving approx. 20% of the original component of lowland open forest (P. Stanton, I. Robb, pers. comms), is highly fragmented, the subject of ad hoc fire regimes and mostly unprotected. Approximately 76% of this remnant is potentially available for future development (45% alienated (i.e. freehold/leased), 31% Crown). *Petaurus gracilis* is poorly represented in the 7% (4841ha) open forest protected by National Park tenure (see preceding), and the remaining significant slice of 16% (State Forest, 10,494ha) is highly fragmented. In late 1992, Queensland Forest Service (QFS) suspended clearing of native forest near Cardwell following the recording of *P. gracilis* in State Forest at Porters Creek. Seven specific areas of the coastal lowlands had been selected by QFS for clearing prior to the establishment of exotic pine plantations (total area 3710 ha). Each area was investigated by the QFS Fauna Conservation and Ecology Section in October 1992 to determine the presence of *P. gracilis* and to allow an evaluation of the conservation significance of each proposed area as *P. gracilis* habitat. Gliders

were detected in 4 of the 7 sites investigated (total area 3050ha) and in locating gliders at Wharps Holding, QFS ecologists extended the known southerly distribution of the species (J. Kehl, pers. comm.).

Core areas predicted by the BIOCLIM system have been mostly cleared from the north and south and replaced along the Ingham-Tully coast by plantation pine (Fig. 32). Records from predicted marginal areas indicate the present day distribution is concentrated near foothills and relic riparian corridors. The extensive area east and south of Barretts Lagoon represents a significant remnant core area.

The endangered status of *P. gracilis* (Van Dyck, 1991) in tropical Queensland should not be regarded in isolation, but seen as symptomatic of a pattern of decline of abundance and extinction repeated across Australia. The threats faced by this glider are not unique to it but shared by the entire tropical coastal lowland woodland ecosystem of which it is one component. In 1982, Tracey commented that his Vegetation Types 18 (Swampy Coastal Plains) and 19 (Coastal Floodplains and Piedmont Swamps) had been either cleared and drained for sugar-cane, or where they had once been common along the Tully River and Murray River were now practically extinct. Braby (1992) reviewed the status and biology of eleven species of butterfly dependent on the Cardwell Basin lowland woodlands and concluded that their habitat ranked among the most threatened habitats in north Queensland. Recher & Lim (1990) presented data suggesting that the decline of vertebrates first observed in southern Australia has extended to the northern parts of the continent and that fauna of the wetter coastal regions may also be affected. They predicted that if such observations are correct, the outcome will be the rapid extinction of species throughout Australia in the next few decades. They recommend that in the conservation of terrestrial fauna, the emphasis needs to shift from species preservation to the management of ecosystems.

'The scale of change is not of individuals or populations, but of functional units of interacting organisms. Once destroyed it is no more likely that an ecosystem can be restored to its original state than an extinct species can be resurrected from its bones recovered from a museum drawer' (Recher & Lim, 1990: 295).

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TABLE 7. Macerals and pollen types identified in faecal samples of *P. gracilis* from Barretts Lagoon, 1991. Frequency: H = high, M = moderate, L = low. Abundance: A = abundant, C = common, R = rare.

Slide contents	Feb	10 May	6 Aug	9 Aug	26 Nov
CONTROL SLIDE (macerai type)					
Pollen	M	L	H	L	M
Other plant mat.	M	H	M	H	H
Insect fragments	M	L	M	M	L
Silica crystals		L			
% pollen with contents	40	50	30	20	20
POLLEN SLIDE (pollen type/ abundance)					
Myrtaceae	A	R		A	A
Banksia		C			
Xanthorrhoea		C	A	C	
Grevillea/Hakea				R	
Acacia				R	

Cook University) who were prepared to work, to be paid, and to smell like slaves during the field component of this survey. Their monumental effort is warmly acknowledged.

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THE PRODUCTION AND DISPOSAL OF PIGS BY KUBO PEOPLE OF PAPUA NEW GUINEA

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In 1986-87, a small community of Kubo people, of the interior lowlands of Papua New Guinea, kept from 0.27 to 0.54 domestic pigs per person. The animals were fathered by wild boars and born to both wild and domestic sows. Male pigs were castrated. For about 18 months each pig was in the care of a particular woman; thereafter, it was released to forage in the backswamps but was regularly monitored by its carer and, like village-based pigs, provided with much fodder, particularly the pith from sago palms. An exceptionally close bond was established between each domestic pig and its carer. Men contributed little to the management of domestic pigs, and carers participated actively when pork from pigs that had been in their charge was distributed. Domestic pigs were not important as a protein source. Their significance was primarily social. On several counts, patterns of production and disposal of pigs by Kubo did not conform to expectations based in earlier comparative and theoretical analyses of New Guinean pig-keeping practices. Kubo patterns are tested within a comparative frame that concerns ratios of pigs to people, work entailed in maintaining pigs, nutritional matters and gender roles. □ *Socio-ecology; animal husbandry; domestic pigs; nutrition; protein; gender roles; Kubo, Western Province, Papua New Guinea.*

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Domestic pigs are important to most New Guineans. They are often focal in the social exchanges that connect different groups of people and, through the time and labour entailed in management, significant in the ecological exchanges that connect people with environment (e.g. Morren, 1977; Rubel & Rosman, 1978). These linked dimensions of the role of pigs were made clear in Rappaport's (1968) classic study among Tsembaga Maring. Indeed, in recent literature that addresses questions of social and agricultural evolution within New Guinea, the place of pigs is central (e.g. Feil, 1987; Kelly, 1988; Bayliss-Smith & Golson, 1992).

Despite the importance of pigs to both New Guineans and anthropological theorists there are few studies that include substantive detail of the husbandry practices of specific groups of people (cf. Boyd, 1984). Notable exceptions are Rappaport (1968), Hide (1981), Boyd (1984, 1985) and Kelly (1988) but these do not capture the full diversity of New Guinean pig-keeping practices (cf. Baldwin, 1990; Yen, 1991). Without an appreciation of that diversity the value of comparative analysis and evolutionary speculation will remain limited (Hide, 1981: 563).

This paper describes the production and disposal of pigs by a small group of people living in the interior lowlands of the Western Province of Papua New Guinea. These people are hunter-

horticulturalists who, on the basis of extrapolating from earlier theoretical literature (e.g. Morren, 1977; Watson, 1977; Modjeska, 1982; Feil, 1987; Kelly 1988; Baldwin, 1990) might have been expected to keep few pigs or none at all, rear only wild-born piglets, raise them on forage rather than fodder, devote very little time or effort to their maintenance and use them to meet nutritional rather than social needs. Kubo people did not conform to these expectations.

KUBO PEOPLE

About 450 speakers of the Kubo language live north and northwest of the Government station at Nomad, Western Province, immediately south of the Muller and Blucher Ranges (Fig. 1; Dwyer, Minnegal & Woodyard, 1993). Between August 1986 and November 1987, with Monica Minnegal, I lived with 25 people at the village of Gwainasi (5°54'S, 142°6'E; 80m ASL) on the west bank of the Strickland River. Our research embraced all aspects of the socio-ecology of the people and earlier reports provide details of environment, subsistence, social life and the historical context within which we worked (e.g. Dwyer & Minnegal, 1991a,b, 1992a). Details of the composition of the village population are available in Dwyer & Minnegal (1993). Here, I summarize

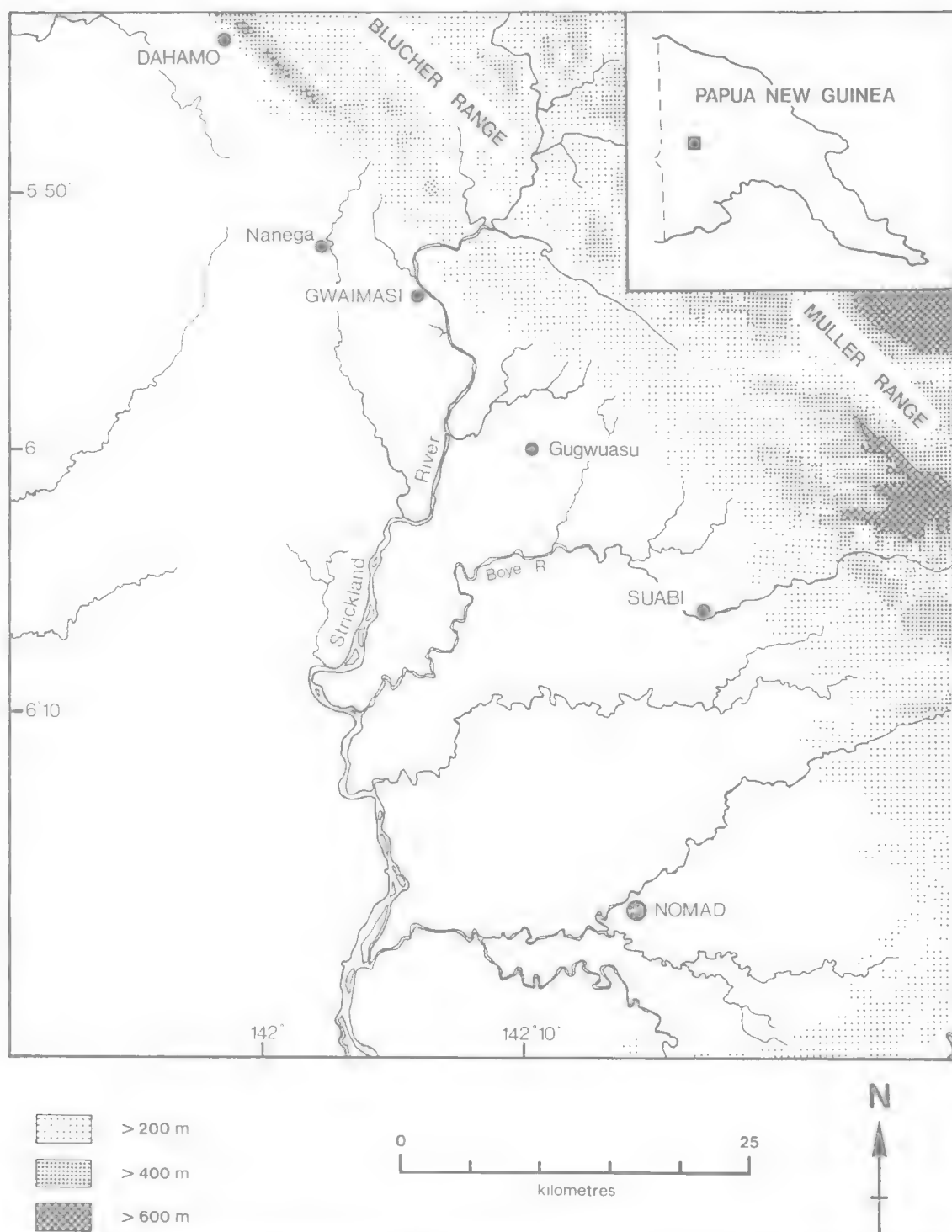


FIG. 1. Location of Gwaimasi and neighbouring communities. The large symbol shows the Government station at Nomad. Small symbols show villages mentioned in the text; names of Gwaimasi and neighbouring mission stations are capitalized.

information that is relevant to reporting matters about domestic pigs.

Gwaimasi village was centrally located within 50 km² of foothill rainforest and swamp forest that was drained by numerous streams and the Strickland River itself. Within this area the residents of Gwaimasi produced their food. Rainfall was approximately 6 m per year with recorded monthly falls never less than 300 mm. The people grew bananas at small unfenced gardens made on levee banks of the river and larger streams, and extracted sago flour from both planted and wild *Metroxylon* palms that were abundant in the backswamps. These carbohydrate foods were of approximately equal importance though at different times one or the other was dominant.

Most protein was derived from animals. Wild pigs and catfish contributed most protein, in terms of weight, but many other vertebrates and invertebrates were included in the diet. Forest products, other than animals, were used as food (e.g. fern fronds, fungi, wild yams and the fruit, nuts and leaves of certain trees) and to fulfil many material needs (e.g. clothing, building and the manufacture of hunting equipment and canoes). Despite the apparent commitment, encouraged by Government and Mission contact, to establish and live in villages Kubo people remained very mobile both within and between local subsistence zones. At Gwaimasi, family groups spent long periods living at forest and garden houses away from the village and often, at these times, had little or no access to garden produce. Since about 1960 there appears to have been increased emphasis upon gardening and less emphasis upon sago extraction to satisfy caloric needs (Dwyer & Minnegal, 1992a).

Dogs and pigs were kept as domestic animals by Kubo. There were nearly as many dogs as there were people and the animals were essential to the successful pursuit-hunting of wild pigs. Domestic pigs, the subject of this paper, were less numerous. My concern here is with what Hide (1981: 406-407) called the 'ecological population': the domestic pigs cared for by a localized group of people within the area that the people themselves routinely traversed. This population need not be identical with the 'sociological population' which comprises the domestic pigs owned by a localized group of people irrespective of where those pigs are located. In New Guinea this distinction is necessary because agistment of pigs is common.

I classed domestic pigs as either 'tended' or 'free foraging'. Pigs in the former category were under almost daily supervision and spent nearly

every night at or near the houses where their carers slept. Pigs in the latter category had been released to forage alone in the backswamps. At different times during its life a pig might qualify as 'tended' or as 'free foraging'. Sometimes a 'tended' pig failed to return to the village for several successive nights. Analyses presented here do not reclassify these cases as 'free foraging'; categorization as 'tended' or 'free foraging' takes the *intention* of the pig's carer to be primary. A recalcitrant 'tended' pig simply increased the work load of its carer who now had to search for it. 'Primary carers' are defined as women who had primary responsibility for particular pigs, wherever those pigs were located, and 'secondary carers' as people who were in charge of pigs for which they did not have primary responsibility. People were classed as carers of 'tended' pigs only if they had been responsible for those pigs through the day and following night. Brief periods of assistance provided during the day are not included in the analyses though they were common. Public perceptions were such that there was no ambiguity concerning the identity of primary carers of 'free foraging' pigs. My classifications of domestic pigs as 'tended' or 'free foraging' and of carers as 'primary' or 'secondary' conform closely with Kubo perceptions.

Most of the data reported below were obtained by monitoring the activities and locations of people and pigs, by direct observation of circumstances of disposal and by asking questions. Estimates of pig weight should be regarded as rough approximations. I did not have direct access to domestic pigs for measurement; the people, but not the pigs, would have tolerated this intrusion. However, where possible, wild pigs were weighed after they were killed and, before weighing, I could usually judge the weight to within 10 percent. Sixteen wild pigs with a weight range from 1.5 to 74.5 kg yielded the following relationship between weight (W = intact weight in kilograms) and mandible length (M = length of horizontal ramus of mandible in millimetres): $\log W = 2.91 \log M - 5.07$. In a few cases this formula was used to estimate the weight of domestic pigs; values obtained in this way are underestimates because domestic pigs were usually fatter than their wild counterparts. Edible weights were estimated as 0.65, 0.70 and 0.75 of intact weight for, respectively, pigs heavier than 10 kg, between 5 and 10 kg, and less than 5 kg.

THE PIG POPULATION

Between September 1986 and November 1987 from seven to 13 domestic pigs were managed by residents of Gwaimasi (0.27 to 0.54 pigs/resident; Fig. 2). These values include piglets only from the date they were removed from sows and taken into the care of women. Piglets that were either eaten ($n = 13$) or exported beyond the Gwaimasi area ($n = 1$) on the day they were taken from a domestic sow were not counted as members of the population.

In September 1986 there were five sows and four large males; four of these animals had been born to domestic sows, the status of the others is not known. Three of the males were confirmed as castrates and the fourth was probably a castrate. One of the sows and two of the males were alive in November 1987. All recruitment during the period of study was as small piglets; five born to local domestic sows, three born to wild sows and one as an import from a neighbouring community. Males and females were included among the recruits but details are incomplete. Losses from the population were four natural deaths at estimated weights of 1.0, 1.5, 4.0 and 12.5kg and seven pigs (15-80kg) killed by people; only the latter were eaten.

Peak biomass of the pig population was in December with about 20kg live weight per resident (Fig. 2). Removals for consumption in January and March halved this value and the combination of additions, estimated growth and losses through the next 7.5 months resulted in only a minor increase in per-person biomass.

MANAGEMENT OF PIGS

At Gwaimasi, all pigs, from the time they were taken from sows, were in the care of women. The 'caring' role was unevenly distributed among available women and was strongly connected with their current reproductive status (Table 1). Caring for pigs was incompatible with caring for a nursing infant. Thus, Wafu and Gogoi did not have 'tended' pigs, Mabei's 'tended' pig was killed six months before she gave birth and the 'tended' pigs of Kose and Bowa were cared for by other women from shortly before Kose and Bowa gave birth, to several weeks after their

infants died. The perceived danger to small infants arose from the possibility that pigs might consume body wastes and proximity between pigs and babies was avoided both at the village and in the forest. (Kubo people believed that an infant's health was placed at risk if its body wastes were eaten by pigs.) Carers assumed the primary responsibility for this, though, in the forest, mothers disposed of their infants' wastes and, at the village, one couple enclosed the area beneath their house so pigs could not reach wastes that might fall through the slat floor. In fact, pigs were not allowed to wander at will within the village area¹.

The married but childless woman Sisigia participated actively as a carer but it was the widow Gogo who contributed most (i.e. 41% and 64% of days associated with the care of 'tended' and 'free foraging' pigs respectively). As a widow who was probably postmenopausal Gogo's lack of direct association with nursing infants was more certain than that of any other woman. One teen-aged girl ceased caring for a young pig at the time of her departure from the village to marry and another, who came in marriage, did not assume the role during the following 10 months. The caring role may have been constrained during early marriage.

The foregoing depicts differential patterns of responsibility but does not reveal the varied nature or extent of those responsibilities. I turn to these matters here, summarizing developmental events in the life of domestic pigs and the work associated with their care.

Domestic sows were impregnated by boars that lived in the backswamps. Of six successful matings, three occurred after our arrival; two of these latter were to a 'free foraging' sow and the last was to a 'tended' sow. The last case shows that insemination by wild boars did not require that sows were managed as 'free foraging' animals (cf. Kelly, 1988: 155).

When births were expected, carers or their agents monitored the sow regularly or, if it was a 'tended' pig, released it into the backswamps or remained with it away from the village. Neither pigs nor women gave birth at the village. Most piglets were captured and either killed or retained when they were from two to four weeks old. In one case a piglet was allowed intermittent access to its mother for a month after capture and, in

¹ Monica Minnegal and I visited Gwaimasi for six weeks in October and November 1991. During the first four weeks there were no children under three years and two large 'tended' pigs often wandered free near the edge of the village clearing. A child was born on November 12, 1991 and, from that time, the pigs were always tethered when mother and child were present.

another, a piglet was left with its 'free foraging' mother for six or seven weeks before it was killed and eaten. Management procedures of these kinds could inhibit return to oestrus by sows and, hence, allow some control over the timing of pregnancies (cf. Hughes & Varley, 1980: 149-151).

Capture of piglets born to domestic sows entailed an overnight stay away from the village by four to six people (female and male) together with some dogs. The presence of dogs resulted in the immediate death of some piglets and injury to others. One badly injured piglet failed to eat sat-

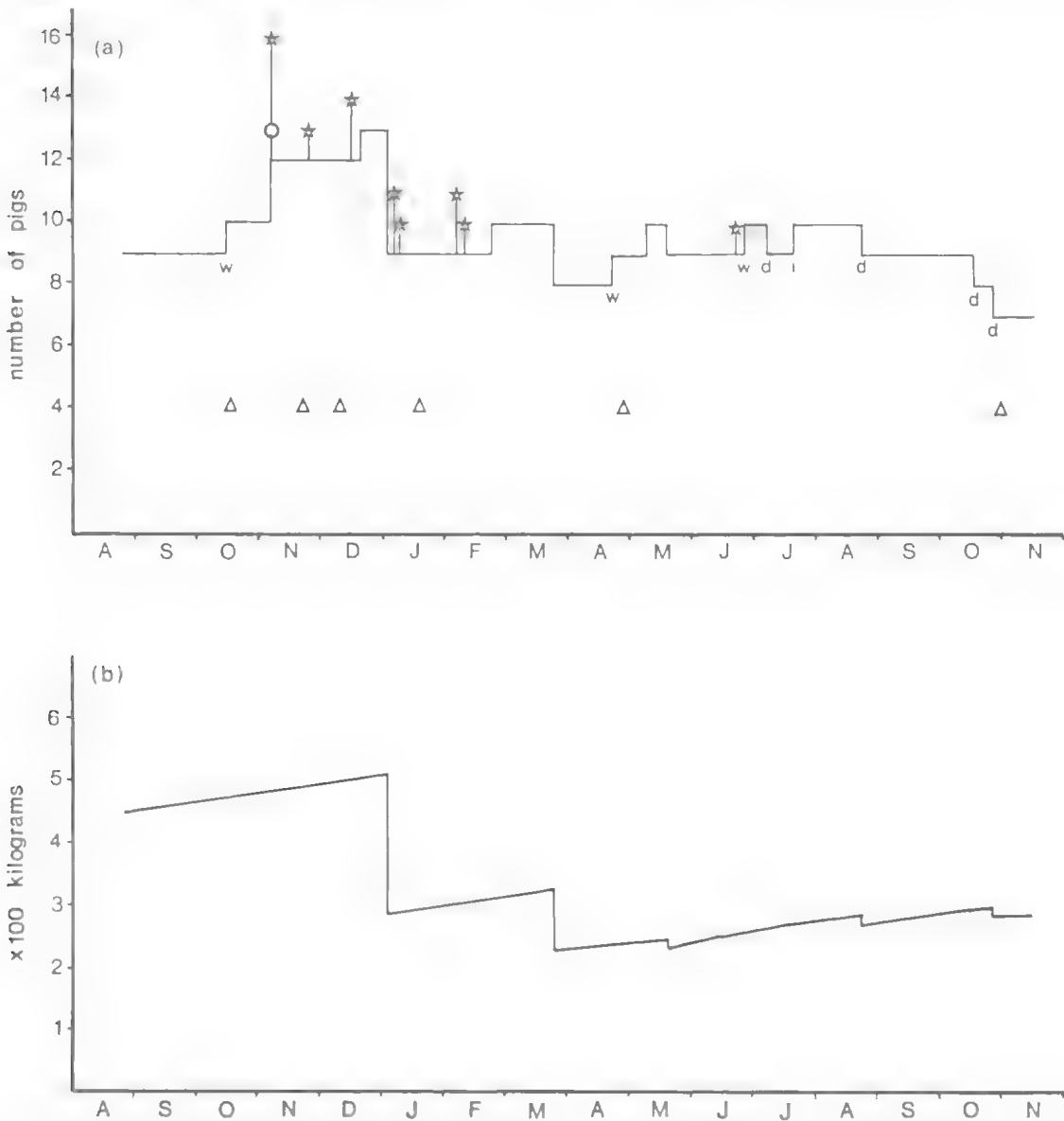


FIG. 2. (a) The size and (b) approximate biomass of the population of domestic pigs; August 1986 to November 1987. In section (a) vertical lines terminating with a star indicate piglets that were captured from domestic sows and killed and eaten on the same day; the open circle indicates one piglet that was exported on the day of capture. 'w' denotes recruitment of piglets born to wild sows, 'i' denotes an imported piglet, 'd' denotes natural deaths and open triangles record the approximate dates on which domestic sows farrowed. Capitalized letters on the horizontal axes code consecutive months.

TABLE 1. The cumulative numbers of days spent caring for pigs by female residents of Gwaimasi: August 25, 1986 to November 15, 1987¹.

Female ²	Age ³	Tended pigs					Free foragers
		1 st carer		2 nd carer		total	1 st carer
		village	forest	village	forest		
Gogo	45	651	327	31.5	6	1014.5	1005
Kose	46	177	84	2	—	263	26
Sisiga	30	330	141	12.5	—	483.5	—
Mabel	25	—	17	6	1	110	441
Gogoi	22	16	—	12	—	28	90
Watu	20	—	—	10.5	13	23.5	—
Bowa	20	230	156	60.5	15	460.5	—
Yasobudua	15	—	—	—	2	2	—
Mugwa	14	68	31	4	—	103	—
Total		1566	756	141 ⁴	37	2500	1562

1. Values are partitioned according to the status of pigs as 'tended' or 'free foraging', as village-based or forest-based in the case of 'tended' animals, and as associated with a primary or secondary carer. All effort associated with pigs classed as 'free foraging' is attributed to primary carers though this does not accurately represent the facts (see text for further details). Half values appear in the table because two women sometimes shared the role of secondary carer. Details are not known for 173 carer-days.

2. Kose gave birth on June 10, 1987 and the child died on July 11, 1987; Mabel gave birth on July 1, 1987 and was lactating thereafter; Gogoi was lactating throughout; Watu gave birth on January 9, 1987 and was lactating thereafter; and Bowa gave birth on July 9, 1987 and the child died the same day. Yasobudua became a resident of Gwaimasi on January 30, 1987 and Mugwa's residency ceased on the same day. The following values record the numbers of 'tended' and 'free foraging' pigs attributed to each primary carer followed by the maximum number of pigs in care at any one time: Gogo 6,3,6; Kose 2,0,2; Sisiga 2,0,2; Mabel 1,1,2; Gogoi 0,1,1; Bowa 2,0,2; Mugwa 1,0,1. When Mugwa departed from Gwaimasi her pig was transferred to Gogo's care.

3. Ages, in years, are estimates only.

4. The caring role was attributed to a visiting woman on one day and to the husband of a primary carer on another.

isfactorily and grew exceptionally slowly during 6.5 months after capture.

For more than a year after capture, pigs were closely associated with carers. For a week or two they were carried, often but not always in string bags, and petted and kissed by their primary carer and other females. From the outset they were trained to accept a lead attached to one front leg and, within a few weeks, would be led to and from the village and allowed to run free when in the forest. But intermittent carrying often continued for three months or more, by which age young pigs had been personally named and were sometimes tethered alone or near another pig in the forest. At about four and a half months their ears and tail were cut and males were castrated, and not until about five months did they spend a day foraging in the forest near the village untethered and unaccompanied by their carer. As long as they remained 'tended' pigs they were usually taken from the village on a lead though, when older than one year, they might often return untethered in the evening.

The precise timing of the events described varied between both piglets and carers. Piglets that grew slowly were treated as though they had aged slowly and some carers were more inclined than others to reduce effort by hastening the independence of pigs. Piglets usually slept in the house of their carer for the first three or four months after capture and were then tethered at night under the house. But, in one case, this bond was not broken until nine months and then only after the carer's husband became seriously ill. Women who prolonged a close attachment to pigs were also more inclined to punish misbehaviour by shouting and smacking; children were never punished in these ways unless, as infants, they defaecated in public.

The bond between pigs and their carers was strong and the effort entailed was considerable. The strength of the bond is evidenced by the minor involvement of secondary carers (Table 1) and by the facts that secondary carers were more likely than primary carers to be resident at the village (79% vs 66%; $P < 0.01$) and less likely than

primary carers to take the pig to the forest to forage (56% of 68 vs 91% of 597 recorded days; $P < 0.001$). When pigs that usually free foraged were located at the village secondary caring was rare (one in 52 observed days) and even the primary carer was unlikely to take the pig into the forest (two of 51 days). Other people's large pigs were difficult to manage; only after about a week of close attention from a secondary carer did even a moderately large pig become manageable.

At the village, carers were responsible for keeping pigs away from the central village area and from small household gardens, for tethering the animals at night and for matters of hygiene (e.g. cleaning sleeping quarters and removing faeces that were dropped when pigs were taken through the village to the forest). Ropes, made from the bark of trees, were made for tethering and as leads and the animals were often groomed by their carer. The pigs also had to be fed. Fodder was usually provided both in the morning and the evening. In addition, pigs were often taken to the forest where they might be tethered, accompany the carer at her pace (on or off a lead) to a place where she intended working or released to forage alone. Pigs were also 'herded', meaning that a carer accompanied by a pig or pigs, travelling at their pace, either took more time than needed to reach a place (e.g. a garden) where she intended working or spent many hours in the forest for the sole purpose of allowing the pigs to forage.

The relative importance of these different management strategies cannot be quantified here beyond noting that pigs were taken to the forest on a minimum of 87% of the days when they, and their carers, were based at the village ($n = 665$). Pig management was often embedded in other activities undertaken by carers and different carers favoured different strategies. Two women who often worked at gardens near the village favoured forest tethering; four others who worked at more distant gardens favoured other strategies. Their preferences were probably influenced by the risk that untethered pigs might return to the village and raid household gardens.

Bananas and the pith (*woko*) from sago palms were the staple fodder provided to 'tended' pigs. (Very occasionally both 'tended' and 'free foraging' pigs were fed fish. Sanio-Hewa and Gadio Enga also sometimes fed small animals to their pigs; Townsend, 1969: 50; Domstreich, 1973: 245) Women who were based at the village nearly always took their pig(s) to places where they processed sago palms; the pigs fed at the accumulating heaps of waste pith. Chunks of *woko* from

these palms were carried to the village and fed to pigs at night; portions were sometimes given to women who had not worked but who had pigs. Other palms were felled as fodder for pigs and large quantities of *woko* were buried in muddy stream beds for retrieval as needed. Again, palms at which flour extraction was completed were visited by women who 'herded' pigs. During 14 months, at least five palms were felled to provide fodder for village-based pigs that, additionally, had access to waste and unused pith from 17 palms processed on behalf of people. Only once did I see sago flour fed to a pig. In this case a woman chewed sugar cane, spat the sweet extract into crumbled flour, and hand fed the mixture to a small, sickly piglet.

When bananas were abundant they were often fed to pigs. They were cooked green, usually by boiling, peeled and sometimes mashed before delivery on a platter to the pig. Between August and November 1986 banana production was low and few were fed to pigs. Thereafter, they were used often as fodder. A tentative estimate is that at least 200 bunches of bananas were fed to pigs from September 1986 to October 1987; this represents six percent of total banana production at Gwaimasi and nearly 500g edible weight of bananas per pig for each day it was village-based (Dwyer & Minnegal, 1993). I did not see ripe bananas fed to pigs, which contrasts with Beek's (1987: 19) observation that Bedamuni, who live to the southeast of Kubo, regarded ripe bananas as fit for pigs (and anthropologists!) but not for people.

The management of 'tended' pigs was less constrained when carers lived at forest houses away from the village. Pigs could forage freely in the forest though they were encouraged to return to the house each evening and were probably usually provided with some fodder. Bananas were seldom available as food - gardens made at a distance from the village had not yielded by the time we departed - but waste and untreated pith from sago palms were available more often than at the village. The pith from 18 palms processed to provide flour was available to 'tended' pigs when they resided with their carers away from the village; i.e. 44 vs 77.5 pig-days per palm when pigs resided at the village. It is likely that additional palms were felled to fodder these pigs.

The management of 'free foraging' pigs was largely invisible to me. Contact was maintained through visits by the primary carer or by a secondary carer who monitored the whereabouts of the pig and reported pending or recent births. Be-

tween December 1986 and November 1987 Gogo visited and remained in the area where two 'free foraging' pigs were under her care on 11 trips totalling 82 days. Similarly, from November 1986 to November 1987, Mabei visited and remained in the area where one pig lived on nine trips (26 days) and Sisigia, who often monitored this pig, visited the area on another 14 trips (39 days). These values exclude day trips to the areas. Activities other than those concerned with pigs were often undertaken during these trips though, in fact, Mabei's 'free foraging' pig was focal to eight of her nine visits.

At least five sago palms were felled as fodder for 'free foraging' pigs and the animals had access to left-overs from at least 15 sago processing ventures (approximately 79 pig-days per palm). Four of the palms were felled during a five month period on behalf of one sow (47 pig-days per palm) and it is probable that the number of palms felled for 'free foraging' pigs greatly exceeded five. At Gwaimasi the pigs classed as 'free foraging' may have been effectively foddered for much of the time though, because the fodder was sago pith, the effort entailed was not great.

By New Guinean standards Gwaimasi pigs were relatively well fed. Estimates suggest that weights in excess of 27.5kg were reached by 60 weeks; at the same age the mean weight of highland pigs from Sinasina, Simbu Province, was 21.6kg (Hide, 1981: 474). Hide remarked that Sinasina pigs grew slowly. All 'free foraging' pigs in the Gwaimasi area exceeded 40kg and two females were 42.5kg and 55kg respectively after birth of their first litters. Hide (1981: 475) reported that sows less than 25kg gave birth in the Sinasina area.

Among Kubo, 'tended' pigs were not released as 'free foragers' until they were about 18 months old and it was only near this age that females attained reproductive maturity (cf. Malynicz, 1970; Hide, 1981: 453).

In October-November 1991, 34 people were classed as residents of Gwaimasi (including one birth and one arrival in the period) and 16 pigs were located in the area. One of these pigs was a five year old barrow. The pigs to people ratio of 0.47 is reduced to 0.40 by including eight people, and one pig, who were formally aligned with Gwaimasi but spent most of their time at Dahamo (Fig. 1) where a primary school was located. Seven of the 16 pigs were 'tended' and one was 'free foraging'. The other eight, owned by members of five families, were in the care of a married couple, who had no children and lived at a fenced

tuber garden on the east bank of the Strickland River. In 1986-87 and in 1991 some 'herds' of large pigs, owned by residents of the mission station at Suabi (Fig. 1), were, similarly, in the care of elderly couples without young children, who lived as much as a day's walk from Suabi. 'Swine-herding' of this sort is certainly a recent practice among Kubo. At Gwaimasi, people said they initiated the practice because pigs were spoiling gardens. This assertion sits uncomfortably with an emphasis on growing bananas, which are not attractive to pigs, with the 1986-87 observation that 'free foraging' pigs seldom spoiled gardens and with the lack of concern that wild pigs were a threat to banana gardens. In addition, the people could have fenced gardens or separated 'free foraging' pigs and gardens by the river without the need that some people lived with those pigs. Hyndman (1979: 212) reported that among Wopkaimin 'all pigs (were) kept in residentially separate pig houses ... or in hamlets used solely for pig raising'. As with Kubo in 1991, these animals were in the care of specially appointed community swine-herds (Hyndman, pers. comm.).

DISPOSAL OF PIGS

From August 25, 1986 to November 15, 1987 449.6kg of domestic pork (edible weight) were available for consumption at Gwaimasi (Table 2). This value includes all the meat from seven pigs in the care of Gwaimasi residents, four pigs in the care of non-Gwaimasi residents and 13 piglets, born to Gwaimasi sows, that were killed on the day they were taken from those sows together with portions of two pigs and one piglet that were carried as gifts to Gwaimasi. Forty-seven percent of this meat was consumed by Gwaimasi residents; an average of 25g per adult-equivalent day of residency (28g with Europeans excluded). The remaining 53% was consumed by visitors to Gwaimasi. The yield of edible meat from wild vertebrates was 255g per adult-equivalent day of residency with 56% derived from wild pigs (Europeans excluded; Dwyer & Minnegal, 1991b). Clearly the total contribution of meat from domestic pigs was minor. Nor was the killing of pigs timed to fill lulls in availability of meat from wild vertebrates; much meat from the latter was available at the time of the feast, on the day before 'nuisance' pigs were killed and on the dates of two curing rituals at which 10kg or more of domestic pork was available (see Table 2).

TABLE 2. Disposal and consumption of domestic pigs at Gwaimasi.

Description	Pigs killed (n)	Days pigs killed (n)	Total kg (edible)	Proportion consumed by residents
Payment to spirit medium	1	1	34.13	0.29
Feast	6	1	292.50	0.37
Curing ritual	3	3	36.24	0.61
Management: 'nuisance'	2	1	63.38	0.76
Management: piglets	12	7	17.40	0.86
Received as gifts ²	3	3	5.95	1.00
Totals	27	14	449.60	0.47

1. Meat was widely and equitably shared by Kubo people. Estimates of the amounts of pork consumed by Gwaimasi residents assume, unless otherwise known (see text), that residents and visitors received shares in proportion to their numbers.

2. Portions of pigs sent as gifts to Gwaimasi; the combined weight of these portions is taken as the total weight.

Of the total edible weight of pork available at Gwaimasi 242.5kg were derived from pigs whose carers were Gwaimasi residents; removal of one pig whose male owner's residency ceased 4.5 months before the pig was killed reduces this value to 206.7kg. The estimate of 210.5kg consumed by Gwaimasi residents is a close fit to these values. However, the proportions of pork contributed and consumed by Gwaimasi residents varied according to the reasons for killing pigs. These reasons are discussed below.

Management considerations (i.e. control of herd size and elimination of 'nuisance' pigs) accounted for the disposal of 11 piglets that were only a few weeks old, one large piglet that for two months had been left with its mother and two sows that, after farrowing, often raided small village gardens. These pigs, all from the local population, contributed 30% of the domestic pork consumed by Gwaimasi residents. Eighty-six percent of the edible weight of the 12 piglets and 76% of that of the 'nuisance' pigs was eaten by residents of Gwaimasi; the latter were killed when the owner of one was visiting and he, with four companions, received a disproportionately large share of the meat.

One small piglet (1.5kg) and two pigs (17 and 40kg) were killed in connection with three curing rituals. The piglet was sacrificed over the heads

of two brothers whose lives were endangered by possible contact with spirits; it was cooked and taken from Gwaimasi for consumption by a visiting male who had danced on behalf of the brothers. At both the other curing ceremonies one hind leg, together with portions of liver and entrails, were needed for ritual purposes (Dwyer & Minnegal, 1988). These portions were subsequently disposed of within the resting place of the spirits of the dead (*toi sa*, forbidden place) through a combination of consumption by bachelor males, burning and throwing to crocodile spirits. Residents contributed 38% of the edible weight of these three pigs and consumed 61%; thus, as hosts to curing ceremonies held on behalf of non-residents, they received more pork than they gave.

On the night before one of the curing ceremonies a visiting spirit medium diagnosed the causes of illness of two people; he received a 52.5kg pig in payment. The animal originated from outside Gwaimasi, was killed and cooked at Gwaimasi and portions amounting to about 10kg edible were given to residents by the spirit medium after he and his son had butchered the cooked meat.

Two medium-sized and four large pigs were killed at a feast on January 3, 1987. These six pigs represented 65% of the total edible weight of domestic pork available at Gwaimasi, and provided 52% of the edible pork consumed by Gwaimasi residents. Residents gave more than they received, contributing 51% and consuming 37% of the edible weight available. The feast was planned several months ahead and preparations were underway in late November 1986. Some people referred to the forthcoming event as *kasimes* ('Christmas', but without recognition of the etymology of that word). Visitors from Gugwasu to the southeast arrived over several days prior to the feast and participated in arrangements. Most residents from Nanega to the west, together with some of their relatives from further afield, made a formal arrival on the evening before the feast. These people had taken several days to slowly lead (and drag!) two large pigs (100 and 120kg) that were to be killed and eaten. This embarrassed the host community which had readied two 'free foraging' pigs, each at 80kg, to feed guests. Two 35kg 'tended' pigs were selected as additions to the intended contribution.

Many of the people who resided at Gwaimasi, Gugwasu and Nanega in 1986-87 had lived together at a different locality in late 1984. This community had split with the primary division being between what became Nanega and Gwaimasi. Nanega was established as a viable commu-

nity and village before Gwaimasi. The feast of January 3, 1987 is interpreted as an assertion by Gwaimasi residents that they now qualified as an ecologically viable and socially self-sufficient community (Dwyer & Minnegal, 1992a). Further, the feast served to reduce lingering tensions that had underlain earlier fission while, at the same time, revealing elements of intercommunity competition. This last was demonstrated as well when, on the night before the feast, two men who were perceived within their respective communities as Government-appointed 'go-betweens' (*komit*) exchanged gifts. The Gwaimasi man, who was acknowledged as 'the owner of the party', gave one tin of mackerel and a kilogram of rice and 'lost face' when, in return, he received twice the quantity of both food-stuffs.

Small quantities of domestic pork arrived at Gwaimasi as gifts from particular individuals; once, from a married man (or from his wife who had cared for the pig) to an unmarried female in acknowledgement of current restrictions on the consumption of terrestrial game and, again, as part of the distribution of a death-compensation payment to a female relative of the deceased person. Details of the third case are not known. In total these gifts comprised less than three percent of the domestic pork consumed at Gwaimasi.

With the exception of some transfers of small piglets all domestic pig transactions among Kubo were as pork and not as live animals. The primary contexts in which these transactions were made concerned statements of intracommunity solidarity, re-establishment of intercommunity relations, the needs of curing, death-compensation and, very importantly, though not witnessed by me, initiation (cf. Shaw, 1990, on neighbouring Samo). In addition, meat was eaten at feasts held to celebrate the completion of new longhouses and often this was pork. Presumably there were also a variety of situations, beyond the few seen, when small quantities of domestic pork were given by one individual to another.

WOMEN, MEN AND PIGS

Among Kubo the role of males in the day to day management of pigs was minor. Certainly, the perceptions of males were that pigs were the responsibility of women and, at the same time, the needs of pigs should not take precedence over the needs of men. It was women who should ensure that pigs did not raid gardens. On one occasion, when a woman cooked food for her pig before doing so for men who had felled trees at her new

garden, a man complained that the work had made him hungry, the woman's priorities were wrong and, after all, the pig had not cut trees!

With women and dogs, men and youths participated in the capture of piglets from sows. At the village, men built secure fences around small yam plots to protect these from pigs (Dwyer & Minnegal, 1990) and it was usually men who felled sago palms used to fodder pigs. Ear clipping and castration were performed by men and they might assist when 'free foraging' pigs, which had come to the village, were returned to the backswamps. Although this last task was not frequent ($n = 9$ at Gwaimasi) it was arduous because these pigs were not at ease on a lead. The male kin of a carer also contributed by monitoring the whereabouts of 'free foraging' pigs, helping build sleeping platforms at forest houses and, of course, through gardening work that produced food that was fed to pigs.

It was not often, however, that males handled pigs or directly fed them. Only on one day was the role of 'carer' assigned to a male (Table 1) and only once was a man seen to collect stored sago pith to feed a pig. More often a carer's spouse might assist by taking a village-based pig to a nearby tether site and, for several months, a pig of more than 15kg was usually lifted by a man into and out of the house where it was allowed to sleep. Underlying this lack of direct engagement of males with domestic pigs was the relative exclusiveness of the bond between a carer and her pig(s); other people's pigs were difficult for anyone else to handle and at times were dangerous to approach. When a pig charged everyone ran! The most common exception to these observations was evidenced by males, especially youths, who sometimes treated small piglets as women and girls did by petting and cuddling them or, less often, taking them from the arms of a female and running off as though to steal. Youths occasionally carried a piglet in a string bag, either through the village or at departure with the piglet's carer and, once, for about 10 minutes, a 15 year-old youth walked a piglet on its lead around the village domain. His behaviour was that of public display; the transvestism was striking and was reinforced later in the day by an extended period of cross-dressing.

Details of the ownership of pigs are incomplete. Pigs were individually owned by both males and females with early teenagers eligible to be owners. Ownership and caretakership could be coincident and, usually, ownership rights went to the person who captured a piglet from a sow, wild or

domestic. One effect of this latter pattern was to disperse ownership and inhibit opportunities whereby particular owners might increase their holdings. Though, of course, both carers and owners of sows could exert some control over ownership patterns by choosing the participants in piglet capturing ventures. Pigs in the care of a woman were, if not her own, more likely to be - but were not exclusively - those of close kin. The widow Gogo cared for pigs that belonged to a clan brother, an orphaned youth with affinal links and an unrelated male. The eventual fate of some pigs in exchange was decided from the time they were piglets and, thus, long-term commitment to the caring role was itself a component of the perceived value of that exchange (Dwyer & Minnegal, 1992b).

The direct role of Kubo carers was considerable when domestic pigs were killed, butchered and distributed. For several weeks before 'free foraging' pigs were killed they were attended more closely than usual by their carer and, eventually, were brought to the village to be closely watched and regularly fed. At initiation ceremonies the need for attention was reduced by caging the pigs

(cf. Shaw, 1990, on Samo). It was a woman, usually the carer, who, at the time of killing, tethered the pig to a stake, calmed it and stood within a metre or two as a man shot it using bow and arrow.

After pigs had been killed, carers moved away as men dragged the carcass to a rack where it would be butchered. Carers were sad but did not grieve openly, though once the widow Gogo sought relief by taking a year-old child from its mother and carrying the infant for 15 minutes or so. (Public grief by females was more evident when a family dog died.) But carers reappeared when men commenced butchery, standing near and sometimes sitting on the rack. They were likely to be the only women in attendance and, in the later phases of butchery when portions were selected for distribution before cooking, often gave forceful instructions to the men (Fig. 3). Carers contributed to the actual distribution of these portions and were sometimes the sole distributors; they also apportioned and distributed entrails, which women had washed, to other women. At this late phase of the precooking butchery and distribution, when most males had



FIG. 3. The woman Kose gives instructions as a pig she cared for is butchered and readied for distribution. A second woman at the butchering rack was a visitor to Gwaimasi who had been primary carer to another pig that was killed on the same occasion.

dispersed, carers might move freely about the rack as they completed a variety of tasks. Women did not contribute to laying the primary oven though some might cook ribs on an open fire for general distribution before that oven was opened. Carers reappeared and observed carefully as men took cooked pork from the oven and they sometimes participated by instruction and action in the apportionment and distribution of this meat after males had carved it.

The participation and rights of carers in the apportioning and actual distribution of pork from domestic pigs were considerable. The almost exclusive bond that existed between carer and pig presumably underlay this. Certainly, the carer was needed at the moment of killing - few other people could have tethered or calmed the pig. However, the extent of female participation varied. It was probably greatest when ownership coincided with caring. It was relatively subdued at more formal events that were attended by many guests or when they, as carers, had come as visitors with their pigs. Again, when two pigs were killed in connection with a curing ceremony that was under the close supervision of a visiting spirit medium, it was he who controlled both carving and distribution after the pork was cooked; there was no contribution from women.

DISCUSSION

This report of Kubo pig husbandry practices is based on detailed observations of a small number of pigs kept by a small number of people. These observations are sufficient, however, to show that Kubo practices were distinctive. They did not fit expectations derived from general and theoretical statements concerning the variety of strategies from New Guinea. In this sense the Kubo case enlarges understanding of the diversity of connections between people and pigs. The primary aim of the following discussion is to locate the Kubo system of pig production and disposal within a comparative frame; to highlight similarities with, and differences from, other New Guinean systems. After brief comparative comment on ratios of pigs to people I discuss (a) the work entailed in maintaining pigs, (b) the importance of domestic pigs to nutrition and (c) connections between pigs and gender roles.

PIG POPULATIONS

Ratios of domestic pigs to people vary widely throughout mainland New Guinea (e.g. Feil, 1987: 45; Kelly, 1988: 150). In broad outline

these ratios are relatively high (0.60-2.0 or higher) among societies of the Central Highlands and some fringe highland groups that are either structurally and ecologically similar to, or interact often with, the former; low (0.10-0.30) among middle and low altitude societies of the rainforested interior that have little or no contact with the Highlands; and variable (0-1.0) among coastal and near coastal societies.

Geographically, ecologically and socio-culturally Kubo may be best aligned with low and mid-altitude societies such as Bedamuni, Baktaman, Wopkaimin, Miyanmin, Hewa, Sambia and Umeda where ratios of pigs to people are less than 0.30 (Gell, 1975; Hyndman, 1979; Herdt, 1981; Beek, 1987; Kelly, 1988: 150). Indeed, their territory is contiguous with that of Bedamuni to the southeast and within 60km of Baktaman to the northwest. Data from 1986-87 and 1991 reveal that Kubo kept more domestic pigs per person than did any of the other societies within this cluster. The recorded ratios of 0.27-0.54 are intermediate between those of broadly similar societies and those of Highland societies. Relative to these societies, however, Kubo are by no means intermediate according to other criteria (e.g. human population density, agricultural intensification, importance of sweet potato, existence of ceremonial cycles in which pork or live pigs are exchanged, or gender relations) that have been sometimes connected with the relative abundance of domestic pigs.

The comparative data from 1986-87 and 1991 suggest that the size of the Gwaimasi pig population in the earlier period was neither an artefact of circumstances prevailing at that time nor solely attributable to the extraordinary performance of one carer. In 1991 it was Sisigia, with her spouse, who acted as swine-herds and who had, in effect, assumed the earlier role of the widow Gogo (cf. Table 1). Gogo, in 1991, acted as primary carer to only one 'free foraging' pig. Again, in 1986-87, there was no evidence that Kubo people had increased the size of pig herds through recent decades in response to diffuse impacts of modernization. This contrasts with Kuchikura's (1990) report that Raiwol speakers, at 1000m altitude in the Upper Murray Valley, have, through the past decade, increased reliance upon sweet potato and simultaneously increased the size of pig populations.

PIG MANAGEMENT

Throughout the Central Highlands and in some fringe areas the absolute densities of people and

domestic pigs are relatively high. Maintenance of pigs in these areas is reliant upon provisioning the animals with food, particularly sweet potatoes, that has been grown for this specific purpose. Kelly (1988) described these systems of pig production as 'fodder-based'; they are labour intensive systems that may vary according to the relative importance of fodder and forage (cf. A. J. Strathern, 1988: 198).

Fodder-based systems of pig production permit relatively high ratios of pigs to people. But in some areas of New Guinea similarly high ratios may be achieved in a different way. Among Etoro, of the highland fringe, and Elema, of the coastal lowlands, human population densities are comparatively low but the ratios of pigs to people are like those seen in the Highlands (Kelly, 1988). The lack of significant human impact on forest habitats provides opportunities to forage domestic pigs on 'wild' foods. In these societies, therefore, after an initial period in which young pigs receive close attention and much fodder from carers they are released to forage alone. Pigs that are managed in this way become bonded to their carers and, particularly, to their usual foraging areas; this severely limits the possibility that they can be exchanged *live* between individuals or groups. Kelly (1988) described these systems of pig production as 'forage-based'; they require relatively low inputs of labour. Kelly used the Etoro case to challenge earlier theoretical argument that proposed direct causal links between the elaboration of Highland socio-economic systems and increases in the relative abundance of pigs.

In many low and mid-altitude areas of New Guinea human population density is low, forage for pigs is presumably abundant but the ratio of domestic pigs to people is low. Kelly (1988) suggested that societies located in these areas underutilize available forage. Instead, they direct minor surpluses of garden produce (or sago) to a relatively small number of mature pigs that might be either confined in cages (e.g. Keraki) or closely bonded to their carers and the normal residential sites of those carers (e.g. Marind Anim, Miyanmin, Baktaman). While agreeing that the availability of forage is not limiting in these areas I think Kelly de-emphasized the importance of forage to the pigs that were kept by societies of the low and mid-altitudes.

Beek (1987: 26) referred to mature Bedamuni pigs that were 'left to roam about in the forest'. Barth (1975: 35) commented that 'fully trained' Baktaman pigs 'can be allowed to roam freely',

Hyndman (1979: 212-213) reported that Wopkaimin allowed domestic pigs 'to spend a considerable amount of time foraging in the Mid-mountain Rainforest and secondary forest' and Baldwin (1982: 36-37) wrote that pigs kept by the coastal Gogodala 'are provided with only a minimum of food' but, rather, forage on scraps within the village area and 'venture into the nearby bush, where ... they seek out and consume such diverse wild foods as fruits, roots, worms, grubs, as well as reptiles and small mammals'. Although, in all these societies, pigs receive some rations directly from people, and, as with Etoro (Kelly, 1988: 116; Dwyer, 1990: 58), may do so through most of their lives, the impression left by most reports from low and mid-altitude societies is that, as with Etoro and as Morren (1977: 294) wrote of Miyanmin, very little human effort is expended on the production of pigs. Management of pigs by Kubo did not fit this generalization.

Management of pigs by Kubo was, at the least, time-intensive. For 12 to 18 months pigs were in the daily care of women. They were five months old before they spent the day foraging apart from their carers; among other low and mid-altitude societies, and in the Etoro case, this is about the maximum age at which the bond between pig and carer is relaxed by releasing the pig to forage alone or with other pigs. 'Tended' Kubo pigs were routinely provided with fodder, though they foraged as well, and, once released to 'free forage' in the forest, were regularly visited and often provided with pith from sago palms that had been felled on their behalf. I suggested above that 'free foraging' animals were effectively foddered for much of the time. The use of sago as a reliable source of fodder for these animals had the effect that their movements within the forest were likely to be localized and, with both 'tended' and 'free foraging' pigs, may have contributed to the moderately high growth rates inferred earlier. Hughes (1970) summarized experimental data that showed that pigs fed on sago gained more weight than others fed on sweet potato; he noted also that the fibrous pith of *Metroxylon* sago, which is favoured as pig fodder, is rich in protein. Certainly, 'free foraging' pigs were noticeably fatter than the wild pigs killed by Kubo men. Most of the latter were taken in the forested foothills; all of the former had lived in the backswamps.

On a day to day basis the management of pigs by Kubo was not labour intensive. About 6% of banana production was directed to pigs; some of this probably derived from bunches of inferior quality. This is less than Morren's (1977: 294)

estimate of 16.2% of Miyanmin garden produce fed to pigs in the form of undersized tubers and scraps and, of course, much less than the estimates of 30% or more of garden produce directed to pigs among societies of the Highlands (e.g. Rappaport, 1968; Waddell, 1972; Hide, 1981). Again, though Kubo pigs were fed much sago, the labour investment here was small. With 'tended' pigs the on-going tasks were providing (and sometimes cooking) food, attention to hygiene, making tether and lead ropes and, with larger pigs, the retrieval of animals that broke tether and wandered free within the village. Carers had much latitude as regards daytime management: they could 'herd' their pigs, which happened sometimes and had the effect that the woman concerned could do little else at the same time; they could tether the pigs in the forest which meant that the tether sites had to be changed several times in the day; or, as happened most often, they could combine the care of pigs with whatever other activity they had chosen for the day. Again, therefore, it was the investment of time and not of labour that was of primary significance in the management of pigs by Kubo. And the important outcome of this pattern of investment was that the bond established between a pig and its carer was exceptionally strong and, effectively, non-transferable. This bond was more important than bonds to specific foraging areas that might be established through long term familiarization with those areas. Domestic pigs sometimes returned from the forest, or crossed the Strickland River, to find their carers; I have no records of pigs returning to favoured foraging areas (cf. Dornstreich, 1973: 244). This argument has implications concerning patterns of management in areas where human populations are relatively mobile (cf. Hyndman, 1979: 212).

Relative to descriptions of pig management practices among other low and mid-altitude societies of the interior, Kubo practices were similar as regards low investment of labour but differed in terms of the much greater investment of time, the importance of fodder (where this includes sago) and a heightened degree of bonding. Except on one count they differed in the same ways from

Etoro. Though Kelly (1988: 119) concluded that Etoro pig-keeping practices 'require minimal labor inputs' he did not refer to the fact that Etoro gardens are fenced and that this task is necessary only because both wild and domestic pigs are strongly attracted to sweet potato. Indeed, at higher altitudes of Etoro territory, wild pigs were rare and all garden fencing (8.27km in 12 months by 109 people; Dwyer, 1990) must be regarded as labour invested in the management of pigs. Thus, among Etoro, the investment of labour in the management of domestic pigs is, in fact, relatively high as, of course, it is among Highlanders who must fence gardens to protect sweet potato².

Among Kubo the investment of time in the care of pigs and the bond established between pigs and their carers were correlated. Both may be linked, at least in part, to the fact that Kubo kept many dogs that were life threatening to free-running piglets (Dwyer & Minnegal, 1992b) and to the necessity to isolate the numerically small domestic population of pigs from the very much larger wild population. Kubo pig management practices constructed 'psychological' fences between domestic pigs and their wild counterparts; without this barrier there might have been no 'domestic' pigs. In fact, among Kubo, the 'tended' pigs of one carer were effectively isolated from those of any other carer; this is not the usual state of affairs elsewhere in New Guinea. Taken overall, this discussion of Kubo management procedures suggests that future comparative analyses should attempt to disassociate the variables of fodder vs forage, time vs labour investment, and bonding to carer vs bonding to foraging area. In earlier studies these have been often treated simplistically. Within New Guinea, there are multiple expressions and many possible combinations of these important variables.

PIGS AND NUTRITION

Pigs feature prominently in proposed explanations of social and agricultural evolution in New Guinea. The central theme of most accounts within this genre is a concern with the emergence and elaboration of Central Highland's formations from precursors in which the social relations

² There is a problem for analysts here. When Kubo people fence their gardens they state that they are doing so to control pigs; it is easy to categorize the work as connected with the management of pigs. But when Highlanders, and Etoro, rotate gardens by enclosing areas within a fence their perceptions appear to be that the work is integral to gardening despite the fact that there would be no need for that work if there were no pigs. Analyses of the division of labour associated with different subsistence domains might reach different conclusions when making fences is regarded as gardening or as pig management respectively. Conclusions might vary also as the perspective of analysis shifts from 'operational' to 'cognized' in the sense of Rappaport (1968).

within and between groups were different and the production of both garden foods and pigs was less intensive (Morren, 1977; Watson, 1977; Modjeska, 1982; Feil, 1987; Kelly, 1988). These accounts differ from each other in the emphases assigned to ecological and social determinants of the context and process of change, in the connections proposed between pig production and expressions of inequality within social groups and, indeed, in situating gender inequality as relatively early or relatively late in the proposed evolutionary sequences.

One theme, however, appears to unite these interpretations: intensification of pig production within New Guinea is thought to be connected with a decrease in the availability of wild animal protein sources. This connection may be explicit or implicit. It is associated with either the earlier phases of transformation (e.g. Morren, 1977; Watson, 1977; Modjeska, 1982; Feil, 1988; see also Golson, 1982) or thought to emerge later as human and pig populations increased in parallel and the demands of the former led to forest reduction and a need to provide pigs with large amounts of garden produce in lieu of forage (Kelly, 1988). The former view, at least, implies that domestic pigs were an important source of supplementary animal protein even in areas where the ratio of pigs to people was low.

At the most, the average daily contribution of protein from domestic pigs was 3.75g per 'adult' Kubo consumer (i.e. 15% of edible meat with consumption values for children adjusted as in Dwyer & Minnegal, 1991b). This is less than 10% of the protein derived from wild vertebrates. In addition, Kubo ate many invertebrate animals, with crayfish, shrimps (*Macrobrachium*) and weevil larvae adding considerably to the intake of animal protein. Meat from domestic pigs was eaten irregularly and there was no suggestion that domestic animals were killed to fill shortfalls in the supply of meat from wild animals. By New Guinea standards, Kubo ate a lot of animals; their protein intake was probably well in excess of requirements and, hence, the minor contribution from domestic pigs cannot be interpreted as having threshold significance.

I conclude that the production of domestic pigs by Kubo was of no importance in terms of protein nutrition. It is likely that, with few caveats, this conclusion applies throughout New Guinea. It may be the case with some societies that domestic pigs are killed and consumed at times when other sources of protein are scarce or, more likely, that other sources, though available, are foregone at

times when domestic pigs are eaten (cf. Morren, 1977: 289). It may be also the case among some Highland societies that protein is generally scarce and the consumption of domestic pigs tips the balance in favour of adequate requirements. But I cannot agree with the statement that for most Highlanders domestic pigs are 'the major source of high-quality protein' (Golson & Gardner, 1990: 396).

The nutritional advantage of animal foods over most plant foods is that the former provide a balanced array of amino acids and, as well, may be the only locally available source of vitamin B12. Some amino acids, often described as the 'essential' amino acids or implicated by statements such as 'complete' or 'high quality' protein, appear to be present in few plant foods. These, together with the more widespread amino acids, must be eaten regularly if human protein nutrition is to be adequate. In New Guinea, pork from domestic pigs is neither eaten in sufficient quantity nor with sufficient regularity to make a significant, on-going contribution to minimal amino acid requirements. Hide (1981: 508) estimated that Waula (Sinasina) people received only 3g protein/person/day from domestic pigs and that, on average, households consumed pork once a fortnight. Through the 12 months of Hide's study the ratio of pigs to people varied between 0.83 and 0.89. Assuming that off-take is proportional to the relative size of local pig populations it is unlikely that the protein contribution from domestic animals approaches 10g/person/day anywhere within New Guinea. Unless it is shown that this is achieved regularly and not, as the literature consistently suggests, very irregularly the conclusion remains unaltered. Norgan et al. (1974) reported high levels of protein intake derived from plant foods among Papua New Guinean Highlanders. Analyses of the amino acid content of New Guinean plant foods are needed to advance understanding of protein nutrition in areas where wild animals seem to contribute little to local diets.

Sorenson (1976: 54) wrote of the Fore that 'sometimes there were periods of several consecutive months without pork, followed by several days of glut after a ceremonial feast'. Occasions of excessive pork consumption are widely reported from Highland societies (e.g. Vayda, 1972: 906). From a nutritional perspective their significance is less likely to concern protein balance than to pose the risk of protein poisoning. Protein foods are potentially toxic unless they are eaten with sufficient quantities of

foods that supply energy (Noli & Avery, 1988; Speth, 1990, 1991). Where protein, from either plants or animals, is used as an energy source then the safe level of intake may fall well below 50% of total calories and, for pregnant females, may be as low as 25% of total calories. Further, high levels of intake of lean meat may be unsafe unless total calories from carbohydrates or fats is increased above normal levels. Noli & Avery (1988: 396), referring to earlier reviews by McGilvery and Speth, wrote that 'when protein is used as the sole source of energy by humans it can lead to nausea and diarrhoea in as little as three days It is also clear from the various case study examples cited by Speth that consumption of lean meat alone led to symptoms of starvation and protein poisoning within a week, diarrhoea within 7-10 days, severe debilitation within 12 days and the possibility of death within weeks'. We were reprimanded often by Kubo when we did not cook sago to accompany meals of pork; the people were not convinced that rice was a sufficient substitute for sago.

Carbohydrate foods and fats provide energy in the diet. New Guineans often reduce carbohydrate intake when pork is available in quantity but they may offset the risk of protein poisoning because they prefer, and in many societies deliberately promote, fat pigs. The thought of fat pigs was keenly anticipated by Kubo. A month before the feast one man exclaimed '*Sori! O wai safai kau*' ('Sorry! The fat of domestic pigs is abundant'). The ethnographic literature from New Guinea abounds with reports of similar statements. Baktaman rub pigs with special white, powdered earth to magically promote fat (Barth, 1975: 35), the ideal Keraki pig was one that grew so fat it could not stand (Williams, 1936: 18), Sanio Hewa castrated all domesticated male pigs 'at a few months of age "to make them lie around and get fat"' (Townsend, 1969: 49) and, for the same reason, Marind Anim kept only barrows (van Baal, 1966: 406). In the Highlands people may prevent sows from breeding or increase the supply of food to pigs as deliberate attempts to fatten animals in readiness for killing (e.g. Hide, 1981). Comparable statements or procedures that extol the value of the *meat* of domestic pigs are very rare.

Throughout New Guinea, whether the ratio of domestic pigs to people is high or low, the significance of the animals is located in the social and not the nutritional sphere. If there are, as well, nutritional benefits then these concern fat more than they concern protein. In the first place, fat pigs reduce the risk of protein poisoning, especially on occasions when much pork is eaten and the normal intake of carbohydrate foods is reduced. Here, the nutritional role of fat is indirect - it is a source of energy that reduces risks associated with eating large amounts of meat. In addition, however, early nutritional surveys within New Guinea consistently reported that fat (including lipids) was poorly represented in local diets (e.g. Oomen, 1971). On this count, therefore, the nutritional significance of the fat from domestic pigs may be also, at some times and in some places, direct.

PIGS AND GENDER

Conventional wisdom has it that among Highland societies inequalities among men and between men and women are intimately tied to patterns of pig production (e.g. Modjeska, 1982; A.J. Strathern, 1982; but contrast with Kelly, 1988). Men strive for prestige. They do so by publicly exchanging valuables, especially pigs and pork. But the labour and time required to rear those pigs has been, for the most part, invested by women. Thus, in pursuit of prestige and leadership, men compete with one another, appropriating the labour of women to their own ends in the process. The outcome is that relations of inequality emerge among males, and women are disenfranchised and disempowered. Under the standard argument these inequalities between individuals and sexes are likely to be greatest where the ratio of domestic pigs to people is highest (cf. Feil, 1987). Indeed, a poignant focus of Highland exchange systems is that, ultimately, the labour invested by women in the production of pigs becomes the means whereby men acquire other women as brides in exchange for those pigs³.

Among Kubo, relations between men and women were characteristically relaxed and warm. There was no ethos of sexual antagonism and little concern with sexual pollution (cf. Sorum, 1984, on Bedamuni). Public expressions of affec-

³ In contrast to the standard argument, Feil (1987: 57-58) asserted that gender inequalities were *least* severe among societies of the Western Highlands where ratios of pigs to people were particularly high and agricultural production was intensive. He thought that 'it is in societies where production and exchange are truncated and streamlined ... that inequalities, especially between men and women in the production process, are the most severe'. M. Strathern (1988) provides a challenging counter to Feil's understanding of gender relations in the Western Highlands.

tion between husband and wife were relatively common (e.g. holding hands, resting in the lap of one's spouse, play-fighting). Aggressive fights were very rare and, for husbands in particular, triggered self-recrimination and a lengthy period of awkward reconciliation. In the subsistence domain, gender roles were conventional and complementary rather than culturally legislated and they were often transgressed. Women sometimes hunted, men sometimes pounded the pith of sago palms and young girls could play with bows and arrows. Though men and women slept in different sections of the communal longhouse, women were not prohibited from entering the men's section. At family houses in the village, gardens or forest there was even less spatial separation between husband and wife.

Kubo women participated less than men in ritual life. They did not dress up and dance as men did (Dwyer & Minnegal, 1988) and, with the possible exception of a focal individual, they (and their pigs) were excluded from seances and the closing moments of curing ceremonies; here, however, the perceived danger was not so much to the women themselves as to infants, including the unborn, with whom women closely associated. But women performed as lead singers and as chorus on all occasions when men danced and, though young women were not initiated, both older men and older women acted as formal sponsors to male initiates. (Among neighbouring Samo, young women were also initiated; Shaw, 1990.)

By New Guinean standards the extent to which female carers of domestic pigs were necessary and active participants when the animals were killed, butchered and distributed was unusual. In ideal circumstances affinal exchanges of pork entailed the simultaneous distribution of meat from two pigs, one contributed by each of the participating groups. This paralleled the ideal of immediate sister exchange as the basis of Kubo marriages. With both the marriages and the exchanges of pork either of the focal women - a bride-to-be or a pig's carer - could veto the intended arrangements. Again, the ideal of simultaneity might not be met because one of the intended partners was judged to be too young or one pig was judged to be too small.

The control that Kubo women exercised over the disposal of domestic pigs may be linked to management practices. The ratio of pigs to people was unexpectedly high and the time devoted to rearing the pigs was considerable. Nearly all the work was done by women and the strategies of management were such that domestic pigs were

so closely bonded to particular carers that the animals were non-transferable. (It seems unlikely that this statement will remain true in the new circumstance of communal swine-herding that is being developed by Kubo.) The permission and physical presence of a pig's carer was perceived as essential when the pig was killed. Though carers were not necessarily owners their engagement with a particular pig persisted through the life of that pig. Because pigs in the care of one woman were effectively alienated from association with other people, and from the pigs owned by those people, there was little opportunity for men to usurp the role of women as the time approached to kill the pigs.

Among Etoro it was the person who completed a process of production who controlled distribution of the product (Kelly, ms.); with domestic pigs it was men who retrieved the animals that were to be killed, who killed and butchered them and who distributed pork at events where other men were the public recipients of the gifts (see also Dwyer, 1990: 130-132). By contrast, among Kubo, women prepared the pigs for dispatch, stood with them as they were killed and officiated at distributions. Their participation was greater and more overt than that described for Baruya women by Godelier (1986: 15-16). From the perspective advanced by Kelly the role of Kubo women is understandable; they were needed to complete the process of production and, hence, shared in the process of distribution. But was that role necessary?

It is difficult to assign either ecological or social imperative to the patterns of pig production and disposal described here for Kubo. There were more pigs than expected and, by comparison with ecologically similar societies, it appears that they could have been managed with far less commitment from carers and with far more latitude for dispersing the caring role. Domestic pigs do not need to be dangerous to people who are not their primary carers! The importance of the animals was not to nutrition but, rather, to the satisfaction of a variety of social concerns. At these events the role and status of women may have been less pronounced if management strategies had been different. The simple conclusion is that Kubo patterns of pig production empowered women and contributed to the markedly egalitarian ethos of Kubo society. This conclusion may seem analogous to that of Feil (1987) regarding Tombema-Enga of the Central Highlands; the analogy, however, would be superficial because any similarities arise within social and ecological contexts that

are entirely different. Both Kubo and Tombema-Enga represent distinct transformations of the commonalities that underlie and unite Melanesian social life (cf. M. Strathern, 1988).

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TWO CAVES

BRUNO DAVID AND LIAM DAGG

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This paper presents results obtained from two archaeological excavations undertaken in the Mitchell-Palmer limestone belt, north Queensland. The sites were excavated in order to investigate temporal patterning in the archaeological record, and especially to obtain information on the antiquity of rock art in the region. In line with previous models of change in Aboriginal prehistory, the results indicate major changes during the mid to late Holocene. They also indicate that the rock paintings from the region may largely date to the last 3500 years, whereas the peckings may be older. □ *Australian prehistory, rock art, north Queensland, intensification, cave paintings, rock engravings.*

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In 1983, Lourandos argued that, in many parts of Australia, major social and cultural changes took place during the mid to late Holocene. Amongst other things, archaeological evidence for these changes include significant increases in deposition rates of cultural materials within individual sites, increases in the number of occupied sites in the landscape, a broadening of resource exploitation strategies (including diet breadth), and major changes in stone artefact technologies. Together, it has often been suggested that these points implied major increases in intensities of site and regional land use (e.g. Hughes & Lampert, 1982). What has been lacking, however, is data to determine the relationship of the separate regional sequences, so as to enable an investigation of the dynamics of structural phenomena, such as inter-regional relations, alliance systems and exchange networks. It is these issues, it is argued, that would enable us to better understand the social contexts of the archaeological changes documented so far.

This paper emanates from these concerns. It presents the results of two archaeological excavations undertaken in the Mitchell-Palmer limestone belt, north Queensland, forming part of a broader research program focusing on the dynamics of socio-cultural (inter-regional) relations during prehistory. In order to investigate socio-cultural structure in prehistory, rock art has been the object of enquiry. Rock art is treated as governed by socio-cultural conventions, so that by investigating continuities and discontinuities in the distribution of rock art through space and time, socio-cultural patterning is itself being in-

vestigated. To shed light on such patterns, a number of sub-regions within north Queensland have been systematically surveyed for rock art sites, thereby enabling an investigation of spatio-temporal trends in rock art conventions.

This paper is a contribution towards these investigations. In order to determine the antiquity of the art, a number of rock art sites were excavated. These excavations enabled the recovery of in situ pieces of pigment (the by-products of artistic endeavours), as well as information on other temporal trends (e.g. stone artefact deposition rates). Together, these data have contributed significantly to our understanding of change and stability in the region.

The aims of this paper are thus to report on excavations undertaken at Hearth Cave and Mordor Cave. In presenting the data obtained from these excavations, broad trends will be revealed, trends that are consistent with those obtained from other sites in north Queensland (David, in prep.).

THE MITCHELL-PALMER LIMESTONE BELT

The Mitchell-Palmer limestone belt consists of a 60km long and 5km wide belt of karst towers (Fig. 1). Caves are abundant throughout the limestone (Fig. 2), two of which were excavated by the author in 1989 (Mitchell River Cave and Hearth Cave). Mordor Cave, located in the Mordor North Tower, was excavated by one of us (BD) in 1991. In all cases, excavation followed the Johnson (1979) method of bucket-spits. All

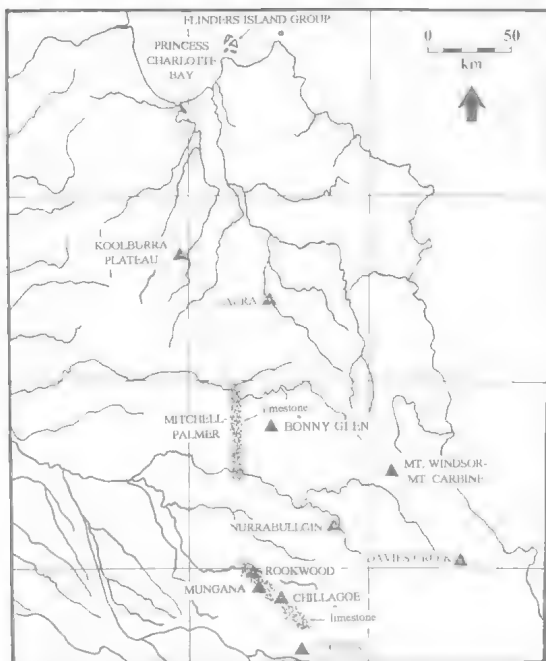


FIG. 1. Southeast Cape York Peninsula, showing location of the Mitchell-Palmer limestone belt in relation to other areas where rock art has been recorded. Arrow points to magnetic north.

cultural materials 2cm maximum size were plotted in three dimensions, and all other materials were sieved in 3mm-mesh sieves. As the results from Mitchell River Cave have already been pre-

TABLE 1. Number of paintings and stencils, Mordor Cave.

FIGURATIVE PAINTINGS		
Anthropomorphs:	vertical	204
	diagonal	8
	upside-down	6
	horizontal	2
Bats		30
Dog		11
Boomerang		3
Pig		1
Crocodile		1
TRACK PAINTINGS		
Bird		4
NON-FIGURATIVE PAINTINGS		
Geometric		22
Other linear		4
Grid		2
Infilled area		2
STENCILS		
Hand		10
Boomerang		1

sented elsewhere (David, 1991a), this paper only documents the Mordor Cave and Hearth Cave data.

MORDOR CAVE

Mordor Cave is a large limestone cave with an uneven, rocky floor located 12 km north of the Mitchell River. It was first rediscovered by L. Pearson on the 17 June 1979, when the Chillagoe Caving Club undertook speleological explorations in the Mitchell-Palmer limestone belt. Mordor Cave was described by the Chillagoe Caving Club Inc. (1988: 43) as having

'three large entrances interconnected with twilight and dark zones linking them horizontally. A peripheral system with some excellent decoration. Aboriginal paintings are executed on walls in mono- and bichrome silhouettes. There are over 140 individual paintings of human figures, dingoes, emus, bats and crocodiles. A pool of water would have served for ochre preparation. Some hand stencils and some inverted figures.'

The main entrance to the cave involves a moderate climb up boulder-strewn pediments, followed by a descent onto a flat floor located near the back wall. It is here that the only occurrence of soft, ashy deposits is located (Fig. 5). On the cave wall are 300 paintings and 11 stencils, most of which are monochrome infilled and red in colour (Table 1, Figs 3, 4). A number of roof collapses give entry to deep caverns along both ends of the cave. Two edge-ground axes and a stone flake were found amongst collapsed material which can be reached by a short walk through pitch-black corridors in these caverns. It is possible, however, that the artefacts were thrown into the collapsed chambers from the skylit chamber above (that is, the main chamber containing the soft ashy deposits).

Mordor Cave was excavated mainly because of



FIG. 2. Limestone karst tower, Mitchell-Palmer limestone belt.

FIG. 3. Mordor Cave, painting of a pig.



FIG. 4. Mordor Cave, main painted panel.

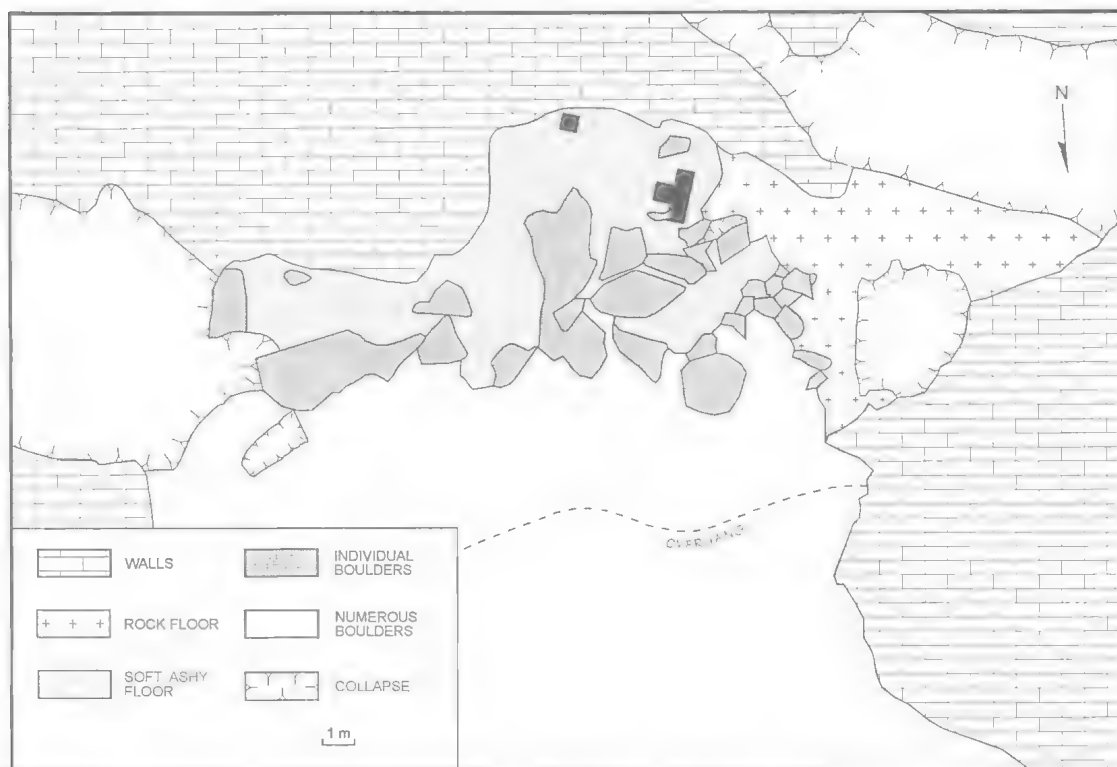


FIG. 5. Mordor Cave, site plan. The arrow points to magnetic north. The excavation squares are represented in infill; Square E18 is the isolated square, and H10 is the centre square of the T-shape excavation.

the large numbers of paintings and stencils on the cave wall, immediately adjacent to soft archaeological deposits. The great numbers of paintings located within a spatially constricted area near soft deposits were deemed to offer great potential for the recovery of in situ ochres, offering the possibility for dating the art by association with dated, in situ ochres. Two test excavations were undertaken in the soft ashy deposits. Square E18 consists of a single 50cm × 50cm pit located near the centre of the soft deposits, where sediments appear to be at their deepest in this part of the site. The main excavation was undertaken 3.5m from square E18, and consists of squares G10, H10, H11 and I10. Square H10 was initially chosen for

excavation because it was located in what appeared to be the deepest part of the site. Squares E18, G10 and H10 were excavated to bedrock, while squares H11 and I10 were only partly excavated in order to enable access into adjacent squares G10 and H10. In total, 1.25m², or 2.0% of the 66m² of soft ashy floor, were excavated. All excavated sediments were very dry at the time of excavation. At some distance from the ashy deposits, closer to the dripline, large lag deposits indicate the existence of drip points and seasonal pools of water.

The excavated materials from squares E18 and H10 have been sorted and analysed and are presented here.

TABLE 2. Stratigraphic Units (SUs) from Mordor Cave, square E18.

SU	pH	Drv	Munsell	Description
1	8.5	10YR	6/2	Surface sediments, grey in colour and ashy in composition. It is loose and appears to be very disturbed. No vegetation appears on the surface.
2	8.5	10YR	6/2	Ashy sediments whose texture is similar to SU1, but with a moderate compaction. Sediments show no evidence of disturbance. No internal stratification is evident.
3a	8.5	2.5YR	3/2	Very dark, black, charcoal-rich sediments with patches of white ash.
3b	7.5	10YR	5/4	Brown silty deposits with a high charcoal content. Very rich in vegetation. Vegetation appears horizontally bedded immediately above the bedrock.

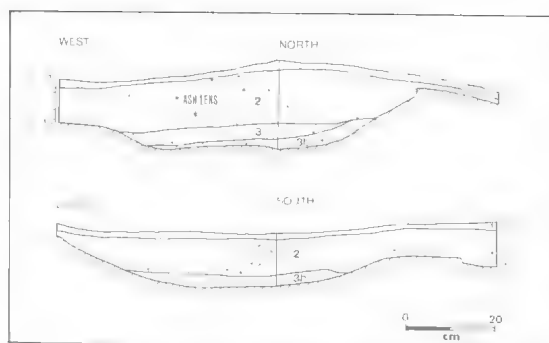


FIG. 6. Mordor Cave, Square E18 stratigraphy. The dots represent pieces of charcoal.

Square E18

Square E18 is well stratified, containing three Stratigraphic Units (SUs), SU3 being further subdivided into two sub-layers (Table 2 & Fig. 6). All stratigraphic units are well defined. Excavation proceeded in seven Excavation Units (XUs), the average thickness of which was 2.6cm.

Square E18 is 20.0cm deep. A single radiocarbon date was submitted from XU7, immediately above bedrock. A radiocarbon date of 1640 ± 70 BP (Beta-46090) was obtained, with a $\delta^{13}\text{C}$ value of -28.4‰ . The $\delta^{13}\text{C}$ -adjusted age of 1580 ± 70 BP is taken to date the beginnings of occupation in this part of the site.

Table 3 presents a complete list of materials recovered from E18. The fauna is listed in Table 4. In Table 5, the raw data have been converted to deposition rates per m^2 per centimetre of deposit, to enable comparisons of deposited materials by XU. Because only a single date was obtained from square E18, the time frames covered by each spit could not be calculated. There-

fore, deposition 'rates' were obtained by calculating the amounts of material recovered per m^2 per centimetre of deposit. These deposition 'rates' are graphed in Fig. 7.

SU1, represented by XU1, contains relatively low amounts of charcoal, bone, land snails, stone artefacts, eggshell, mussel shell and ochre. The proportion of burnt eggshell is also low. Compared with underlying SU2, the sediments contain large amounts of organic material (especially twigs and bark), and compaction is relatively low (as measured by weight per volume). These findings are not surprising given that, firstly, the site is not believed to have been occupied during the last 100 years, and secondly, that the surface sediments were very loose during excavation.

SU2, represented by XUs 2-5, contains large numbers of stone artefacts, land snails, eggshell, mussel shell, ochre, charcoal and burnt earth. Quantities of all cultural materials are relatively low towards the lower boundary of SU2. This may indicate that a hiatus is represented at the SU3-SU2 boundary, or that XU5, the lowermost XU from SU2, should be treated as an interface between SU3 and SU2. This interface should be treated as comprising of intermixed SU3 and SU2 materials.

SU2 contains relatively compact sediments and relatively low amounts of organic materials (mainly vegetation), except for XU5. Here, the organic content is similar to that from underlying SU3a. This further re-enforces the likelihood that XU5 contains materials from the underlying stratum.

SU3a is represented by XU6. It is rich in stone artefacts and bone, but relatively poor in all other cultural materials. Sediments are very compact

TABLE 3. List of materials excavated from Mordor Cave, Square E18.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	1	395	6.5	7.0	127.5	264.3	1.9	3.9	0.25	2.8	76.1	33.3	30	5.9		0.20	1.6	1		0.6	56	8.5	670	4	
2	2	276	4.5	5.0	164.7	131.7	2.2	1.8	0.25	2.9	25.5	20.6	10	2.8	1	0.28				0.2	8	5.6	348		
3	2	675	6.3	6.0	358.4	100.0	4.3	2.1	0.24	2.9	69.3	16.8	23	58.0		2.52	1.1		1	0.2	28	9.9	648	4	11
4	2	216	5.3	5.0	324.9	129.9	1.4	2.8	0.23	9.5	48.5	31.8	10	13.7		1.37	21.9	1		0.2	20	6.0	412		
5	2	313	5.0	5.0	190.8	231.4	1.2	2.3	0.22	1.7	22.4	29.0	19	12.9		0.68	1.3	1		0.3	21	2.9	198		78.6
6	3a	208	5.3	3.5	111.1	160.7	0.8	2.4	0.18	0.3	14.6	28.6	37	27.2		0.71				0.5	42	0.6	59		
7	3b	37	0.8	1.0	67.7	53.2	0.2	2.9	0.13		4.1	4.5	27	8.8		0.33				0.1	2	0.1	3	1	

1=residue >3mm (g); 2=sediments excavated (kg); 3=sediments excavated (litres); 4=charcoal (g); 5=other organics (g); 6=land snail (g); 7=mean thickness of XU (cm); 8=area excavated (m^2); 9=mussel shell (g); 10=burnt earth (g); 11=bone (g); 12=flaked stone artefacts (#); 13=flaked stone artefacts (g); 14=fungus (#); 15=mean weight of flaked stone artefact (g); 16=ochre (g); 17=ochre showing no use-wear (#) (all are red); 18=ochre showing use-wear (#) (red); 19=burnt egg shell (g); 20=burnt egg shell (#); 21=unburnt egg shell (g); 22=unburnt egg shell (#); 23=seeds (#); 24=burnt stone (g).

TABLE 4. Mordor Cave faunal remains: Minimum Numbers of Individuals (MNI), Square E18 (after Dagg, 1992). Question marks indicate the presence of identified species which are believed to be post-depositional intrusions into that unit (for reasons outlined in Dagg, 1992). P=present.

Species	SU1	SU2	SU3a	SU3b	Total
<i>Macropus agilis</i>	1	1	?	0	2
<i>Petrogale</i> sp.	1	2	2	?	5
<i>Trichosurus vulpecula</i>	1	?	1	?	2
Peramelidae	1	1	?	0	2
<i>Macropus gigas</i>	0	1	0	0	1
<i>Uromys caudimaculatus</i>	1	2	0	1	4
Other Muridae	3	9	1	1	14
<i>Canis familiaris</i>	0	1	0	0	1
Agamidae	0	1	0	0	1
Scincidae	0	4	0	0	4
Boidae	0	1	0	0	1
Teleostomi	3	3	1	0	7
<i>Velesunio</i> sp.	P	P	P	P	
<i>Xanthomelon</i> sp.	P	P	P	P	
<i>Alectura lathamii</i> egg	P	P	P	P	

and contain very high amounts of vegetation. The percentage of burnt eggshell is very high.

SU3b (XU7) contains low amounts of all cultural materials except for stone flakes. Sediments are not as compact as overlying SU3a, and their organic content is low. The percentage of burnt eggshell is very high.

The part of Mordor Cave represented by Square 18 is interpreted as having been first occupied approximately 1500 years ago. At that time, occupational intensities were low. During SU3a times, large amounts of organic material, including bark and twigs, were laid horizontally on the cave floor. This layer is well defined, and associated with a low deposition 'rate' of all cultural materials, except for stone artefacts and bone. Stone artefacts are very small, averaging 0.7g. These factors indicate that the sediments recovered from SU3a may have been a sleeping mat,

and that during this time the area was used as a sleeping area. It is therefore possible that contemporaneous materials from other parts of the cave would reveal complementary, specialised activity areas, such as hearths and stone artefact manufacturing areas.

During SU2 times, Square E18 witnessed relatively intensive deposition of cultural materials. It is during this time that most of the paintings on the walls were probably undertaken, as indicated by peak ochre deposition rates during this time. Fires lit during SU2 times may have caused the high proportions of burnt eggshell in XU6 and XU7 underneath. As eggs cannot be roasted directly on a fire (or they would shatter or explode; L. Hughes, pers. comm., 1992), burnt fragments of eggshell are likely to represent subsequent burning by overlying hearths.

The well preserved sediments also contain one large bracket fungus (Fig. 8). It is a single sporocarp of a member of the order Aphyllopharales, family Polyporaceae. It is probably from the genus *Polyporus*, and possibly *P. udus* (P. Bostock & C Young, pers. comm., 1992). The dryness of the cave, and the compaction of the sediments, indicate that it could not have grown in the deposits, but must have been introduced into the cave. Such fungi are known to have been eaten by Aborigines in north Queensland during ethnographic times.

SU1 times include the post-contact period, including the recent period when the site was abandoned. Consequently, the low densities of cultural materials during this time are not surprising.

Square H10

Square H10 is 114.5cm deep, containing four distinct Stratigraphic Units, some of which are further sub-divided into a number of sub-units (Fig. 9). The SUs are described in Table 6.

TABLE 5. Mordor Cave, Square E18: deposition rates (per m² per cm of deposit), and proportions of burnt eggshell.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	1	6.7	6.1	1.95	130.8	78.1	30.8	6.1		7.2	1.6	2.9		271.1	744.6	9.3	6.6	4.1	34.2
2	2	10.0	5.8	4.89	366.0	56.7	22.2	6.2				6.4	2.2	292.6	791.1	12.9	3.4		45.8
3	2	12.5	9.7	8.53	711.1	137.5	45.6	115.1	2.2	2.0	2.2	5.8		198.4	1341.3	20.0	2.0	7.9	33.3
4	2	8.3	3.9	2.17	504.5	75.3	15.5	21.3		1.6	34.0	14.8		201.7	670.8	9.6	4.6		49.4
5	2	9.9	5.9	2.37	377.1	44.3	37.5	25.5	155.3	2.0	2.6	3.4		457.3	235.2	6.3	9.4		57.3
6	3a	12.3	3.8	1.85	257.2	33.8	85.6	63.0				0.7		372.0	233.8	2.6	45.5		66.2
7	3b	2.1	4.4	0.53	179.6	10.9	71.6	23.3						141.1	13.3	0.5	50.0	2.7	11.9

1=sediments excavated (kg); 2=% residue >3mm; 3=land snail (g); 4=charcoal (g); 5=burnt earth (g); 6=flaked artefacts (#); 7=flaked artefacts (g); 8=burnt stone (g); 9=ochre (#); 10=ochre (g); 11=mussel shell (g); 12=fungus (#); 13=other organics (g); 14=egg shell (#); 15=egg shell (g); 16=% egg shell burnt (by weight); 17=seeds (#); 18=bone (g).

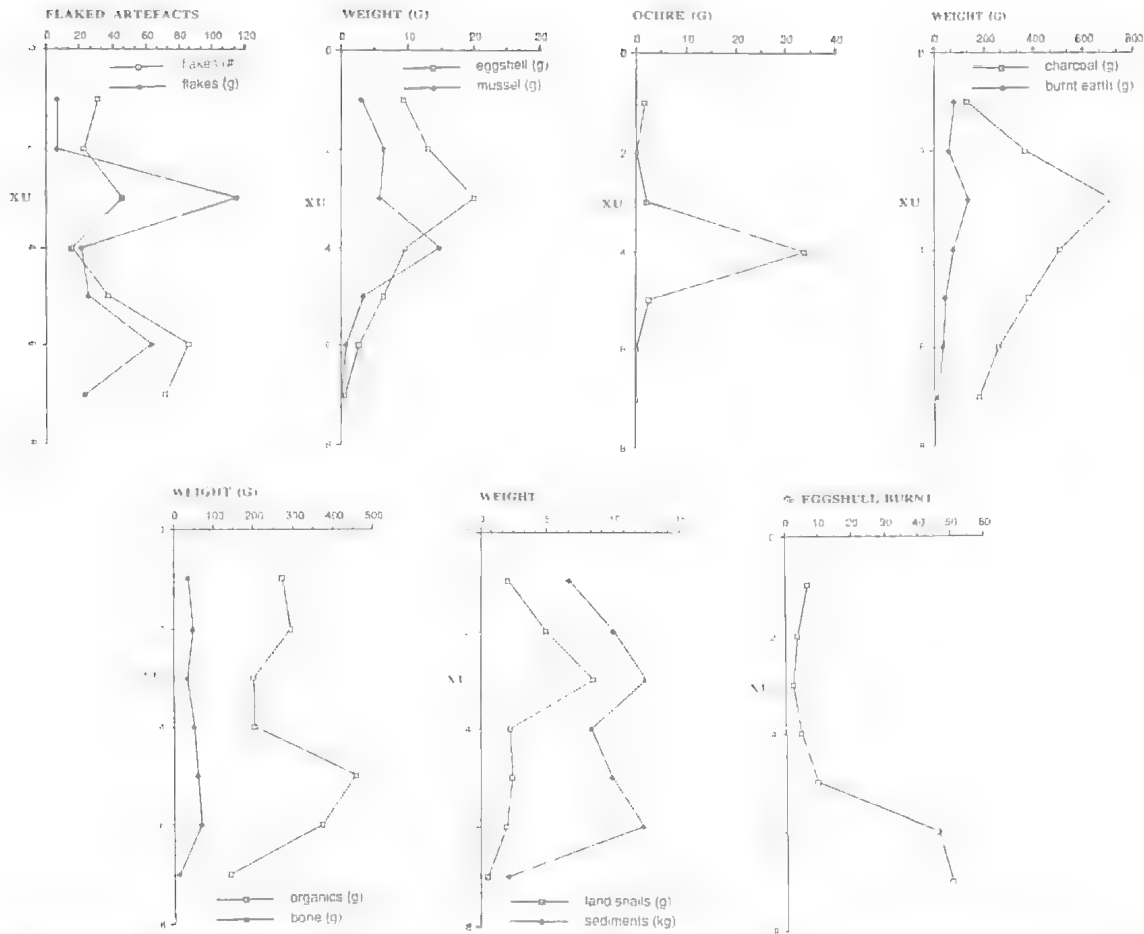


FIG. 7. Morden Cave, Square E18, deposition rates (per m²/cm of deposit) and proportions of burnt eggshell

Two radiocarbon dates were obtained from Square H10: 980±60BP (Beta-46317), located 84.7cm below the ground surface, in XU25 (SU4). The $\delta^{13}\text{C}$ value equals -27.6‰, and the ¹³C-adjusted age is 940±60BP; and 850±50BP (Beta-46318), located 114.0cm below the ground surface in XU28 (SU4). The $\delta^{13}\text{C}$ value equals -28.2‰, and the ¹³C-adjusted age is 800±50BP.

The two radiocarbon dates are similar and overlap at two standard deviations. They are taken to confirm the impression gained during excavation, that SU4 is an archaeologically instantaneous event.

Square H10 was excavated in 28 spits, XU10 of which was excavated in three sections (XUs 10a, b & c). Table 7 documents the amounts of materials excavated from square H10, Table 8 presents the deposition 'rates' as calculated per m² per centimetre of deposit (Fig. 10), while Table 9 lists the fauna identified from square H10.

SU1: this unit consists of XU1 and XU2. It contains relatively large amounts of charcoal, burnt earth, stone artefacts, mussel shell, eggshell, seeds and other vegetation. In short, SU1 represents a peak in deposition rates of a number of cultural materials.

SU3: this unit consists of XUs 3-6. It contains varying but relatively low amounts of cultural materials. XU7 is an interface between SU3 and SU4.

SU4: this unit consists of XUs 8-28. The lowermost seven XUs (23-28) are from SU4h, which appears to be a localised variant of SU4, containing leaves and seeds amongst a rich vegetation (especially bark and twig) matrix. Leaves do not occur above XU22. Whilst SU4 contains similar amounts of cultural materials to SU3, SU4h contains significantly higher amounts of bone and a greater proportion of burnt eggshells, with ochre and pandanus nuts occurring exclusively in this

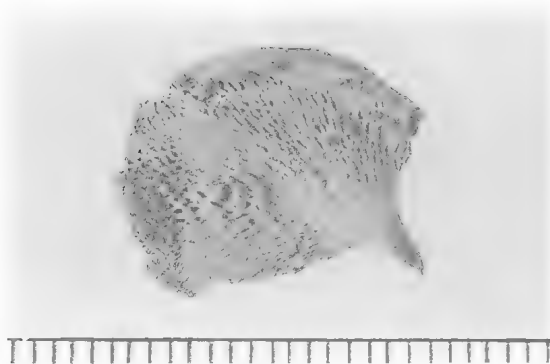


FIG. 8. Bracket fungus found in XU2, Square E18, Mordor Cave (scale in 2mm units).

unit. Amounts of charcoal are more variable between XUs of SU4h than is the case in SU4 proper above it. SU4h sediments contain a relatively high proportion of sediments over 3mm in minimum size, although stone artefacts are very rare. Interestingly, XUs 20-21, located near the boundary of SU4 and SU4h, contain 98.2% of the burnt stone recovered from Square H10. Given that

relatively high percentages of burnt eggshell, as well as consistently high amounts of charcoal and burnt earth also appear in this part of the excavation, SU4 and SU4h may be related to a hearth. This is also supported by the fact that some of the vegetation making up the organics from SU4 is partly burnt. SU4 and SU4h may therefore represent materials dumped when a cooking hearth was emptied to retrieve the cooked food. However, while this explanation would explain the 'instantaneous' appearance of the deposits and the burnt material, it does not account for many of the cultural remains within SU4/4h (see below).

A number of wooden objects, including a digging stick (from XU22) and a large sheet of cut bark containing a number of pandanus nuts around and on top of it (XU25), were also located within SU4 (Fig. 11). A grinding stone with two ground surfaces was also recovered from XU 26. All of the ochre (3 white pieces, totalling 1.4g), none of which contained use-striations, came from XU25 and XU27. A fig (*Ficus virens* var *sublanceolata*, *F. obliqua*, *F. platypoda*, *F.*

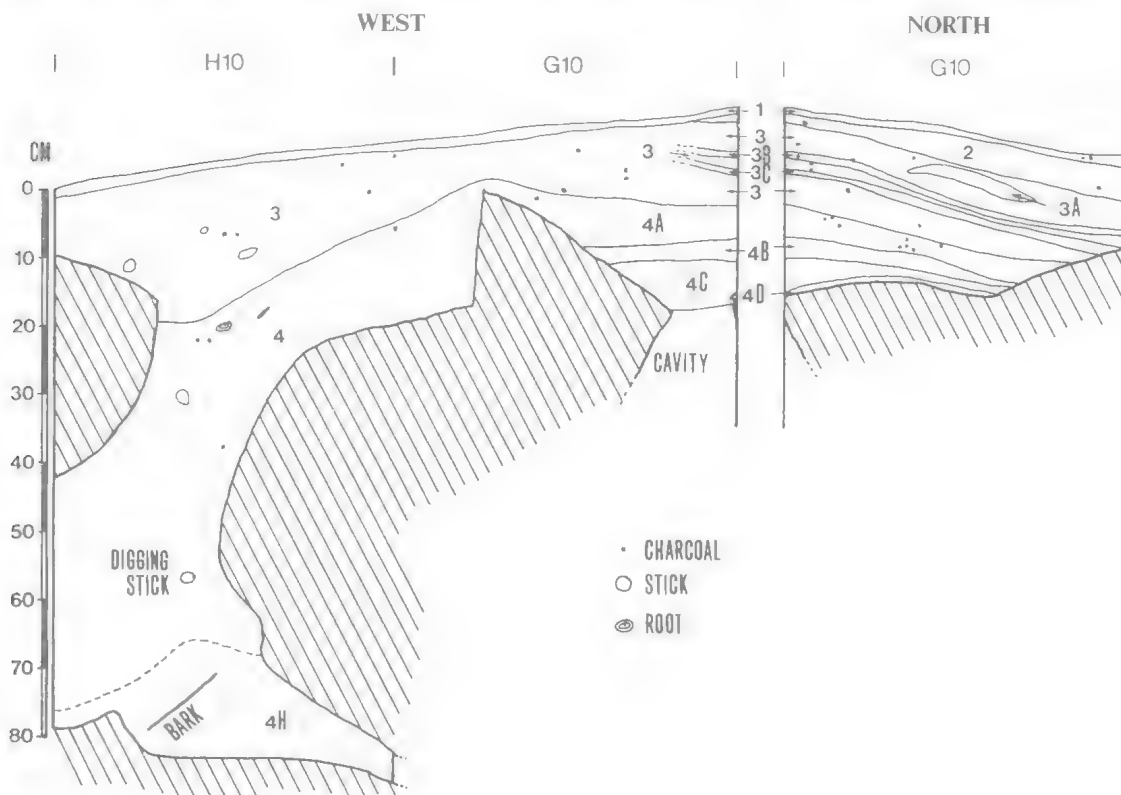


FIG. 9. Mordor Cave, Square H10 stratigraphy.

TABLE 6. Stratigraphic Units (SUs) from Mordor Cave, square E18.

SU	Dry	Munsell	Description
1	10YR	6/2	Loose, disturbed, grey, asy.
2	10YR	6/3	Some vegetation present especially in some parts of Square G10. Brownish-grey in colour. Ashy and moderately compact
	10YR	6/2	Ashy, grey
3a	10YR	6/2	Localised lens of vegetation
3e	10YR	6/3	Well-defined, fairly compact
3c	10YR	6/3	Well-defined, fairly compact
4	10YR	5/1	Very rich in vegetation. This unit contains very little sediment apart for the matted vegetation
4a	10YR	6/3	Dark grey vegetation sub-layers
4h	10YR	5/1	A grey vegetation sub-layer.
4c	10YR	6/3	Dark grey vegetation sub-layers
4d	10YR	5/1	A grey vegetation sub-layer.
4e	10YR	6/3	Dark grey vegetation sub-layers
5	10YR	6/2	A grey ashy unit.
5e	10YR	7/2	A grey vegetation sub-layer.
4f	10YR	5/4	A brown vegetation unit

racemosa, *F. opposita* or *F. coronulata*; *P. Bos-tock*, pers. comm., 1992) was also retrieved from XU23. The fruit contains the dried, soft tissue, and shows no evidence of fully developed seeds (Fig. 12). All of these items come from SU4h or the SU4-SU4h interface zone, indicating that SU4h may have been a different depositional unit to SU4. Coupled with the fact that all of the pandanus nuts and leaves also come from this unit, SU4h is interpreted as having been laid immediately before SU4 was deposited. This took place sometime around 900 years BP. The most parsimonious explanation for SU4/4h may thus be that the vegetation-rich SU4h was laid together as a single unit. This involved wedging vegetation between boulders devoid of underlying sediments, thereby creating a localised 'false floor'. The digging stick, sheet of cut bark, and the pandanus nuts were then placed on top of this matted vegetation layer, and the whole lot was then covered with more vegetation (containing some hearth remains). The reasons for this are unknown, but ethnographic parallels are known from the Mitchell River delta (pers. obs., 1992). Here, Aboriginal people are known to bury people's 'rubbish' (including cherished material items) after their death. It is possible that the Mordor Cave SU4/4h layer relates to a similar practice, although this is, at this stage, mere speculation.

Discussion of Mordor Cave

An interesting parallel between both Squares E18 and H10 is the large amount of vegetation

recovered from the excavations. Especially important is the presence of a bracket fungus from XU2 of Square E18, and a fig from XU23 of Square H10 (dated to approximately 900BP). The very large numbers of Brush Turkey (*Alectura lathami*) eggshell recovered from both squares and from all SUs may also indicate that the site was used on a seasonal basis, and that it was repeatedly re-occupied during the same time of the year (August-December). 2515 fragments of eggshell were excavated from square E18, and 2340 pieces from square H10, distributed throughout the excavated sequences. A single Brush Turkey feather was also recovered from H10 XU3 (Fig. 13).

It is difficult to relate the E18 stratigraphy to that of H10 given the insufficient number of radiocarbon dates obtained. Nevertheless, the peak occurrence of ochre half-way through the deposit in Square E18, whose base was dated to 1500BP, equates well with peak ochre deposition rates around 900BP in Square H10, and may indicate that most of the paintings at the site were undertaken around that time. There is no evidence for any rock art activity at the site having been undertaken before approximately 1500BP. Nevertheless, the presence of a painted pig indicates that cave painting continued into contact times.

HEARTH CAVE

Hearth Cave is located towards the northern end of the Mitchell-Palmer limestone belt, 9km south of the Palmer River. It was recently rediscovered during speleological explorations by the Chillagoe Caving Club, who report (1988:62):

Located on 01/04/83 by M. Andersen on north eastern end of tower A phreatic slot leading back into tower, 3m wide at entrance. Floor is moss and fern covered. Slot develops to the rear far enough to provide shelter from rainfall. In the small narrow section at the back is a significant ash pile, 2m by 2m and 200mm to 300mm higher than the rest of the floor. Eroded sections of this floor shows evidence of broken bones, a possible kitchen midden.

The walls have a number of Aboriginal paintings, some superimposed on each other on the left hand wall. Observed were a boomerang in white and other paintings vertical scrapings with small numbers at lesser angles. They have been apparently made by someone standing, as they are in easy reach at waist level to hand outstretched in height. Exposure is 2m long by 1m high. Right hand side has scrapings, 12 or so scratches but nothing of real significance. Cave is an archaeological site.

Subsequent recording of the site revealed a greater number of paintings and engravings than initially outlined by the Chillagoe Caving Club,

TABLE 7. List of materials excavated from Mordor Cave, Square H10.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	1	279	4.7	5	103.0	148.2	1.7	0.7	0.25	8.6	61.8	16	20.2				0.3	13	1.4	109	1								
2	1	97	1.7	2	36.4	135.3	1.0	0.3	0.25	0.5	17.3	3	0.4				0.1	10	0.4	46	3								
3	3	393	6.3	6	255.0	158.2	5.1	1.9	0.25	1.4	64.5	22	3.5				0.3	28	2.5	185									
4	3	386	5.7	6	106.1	188.6	3.9	1.8	0.25	1.2	27.4	6	7.5				0.4	26	1.5	137									
5	3	339	6.2	7	124.2	255.6	2.8	2.7	0.25	1.7	53.1	7	1.7				0.2	24	2.4	173	4								
6	3	554	7.6	8	234.0	220.0	6.3	2.9	0.25		60.6	9	7.9	1			0.1	20	4.0	238	4								
7	3/4	481	7.0	7	188.6	178.6	4.0	3.2	0.25	1.6	59.8	20	5.4				0.2	17	3.5	216		2.1							
8	4	371	4.6	7	94.2	240.8	3.9	1.8	0.23	2.6	48.6	13	3.6				0.1	9	2.5	146	1			1					
9	4	159	3.2	3	111.7	155.4	3.3	4.0	0.19	1.3	32.7	3	0.3				0.1	13	1.4	99	1								
10a	4	157	2.7	3	52.6	119.4	2.6	4.1	0.09	0.8	25.9	9	2.1				0.1	8	1.4	83									
10b	4	13	0.3	1	16.4	69.6	0.1	2.8	0.01	1.5	3.9	1	0.4						<0.1	1	4								
10c	4/4f	25	0.5	1	16.1	21.3	0.1	2.9	0.03	0.4	5.9	1	0.2				0.1	6	0.2	8	1								
11	4	199	3.6	4	60.9	213.3	3.5	2.5	0.14	0.7	49.0	6	2.4				0.1	10	1.5	93	2								
12	4	209	3.5	4	85.3	390.6	1.2	4.5	0.12	1.0	33.2	3	1.8				0.1	6	1.7	91	3								
13	4	195	3.5	4	153.4	329.7	1.1	5.1	0.11	2.4	56.8	5	2.3				0.1	9	1.1	74									
14	4	159	3.0	4	99.0	258.4	1.3	3.8	0.10	2.4	19.6	7	5.8				0.1	10	0.8	47									
15	4	92	2.2	3	62.5	213.3	0.8	2.7	0.09	0.1	23.0	2	0.1				0.1	5	0.8	26									
16	4	107	2.5	3.5	61.8	189.8	3.4	3.5	0.09	0.5	24.9	6	2.7				0.2	10	0.4	26									
17	4	811	3.5	4.5	55.3	263.5	2.0	4.7	0.09	1.8	19.4	7	4.3				0.1	7	0.1	15									
18	4	162	2.5	4	121.0	249.8	5.9	5.2	0.09	4.5	6.6	2	0.6				<0.1	2	0.1	15									
19	4	88	1.8	3	15.2	318.6	4.9	5.4	0.07	4.5	11.0	3	3.3				<0.1	3	0.1	14									
20	4	146	2.1	5	29.9	277.8	2.8	4.5	0.07	1.3	14.8	4	0.7				0.1	5	0.2	27		36.9							
21	4	221	2.6	5	72.8	224.1	2.6	4.2	0.07	0.2	20.0	1	0.1						0.1	11	1	238.6							
22	4	405	3.3	5	101.8	326.3	3.7	8.2	0.07	2.0	14.1	3	0.1				0.1	7	0.2	29	2		1		1				
23a	4/4h	71	?	?	34.6	242.5	0.4	5.8	0.06	1.3	5.9	1	0.1		<0.1		0.1	2	0.3	17	1		2						
23b	4h	3	0.3	0.1	1.5	3.1	<0.1	1.4	0.01		0.4												1						
24	4h	227	2.8	9	94.9	456.5	0.7	3.9	0.07	0.2	13.4	1	0.1		0.6				0.4	10	2		1					2	
25	4h	32	0.1	3	51.6	184.0	4.7	4.2	0.08	0.3	5.9					0.3	<0.1	1	0.3	4		2.9	1			1			
26	4h	185	4.1	9	212.3	455.9	2.9	5.5	0.16	0.7	18.2				0.2		0.1	7	1.3	54	1		5				1	610.4	4
27	4h	771	3.8	5	41.2	282.8	8.3	6.1	0.18	6.6	19.6	8	2.0			1.1	0.1	4	1.2	42	5		1					1	
28	4h	280	2.5	3	36.7	210.6	1.5	12.6	0.22	3.8	14.8	2	0.6						1.1	42	2								

1=residue >3mm (g); 2=sediments excavated (kg); 3=sediments excavated (litres); 4=charcoal (g); 5=other organics (g); 6=land snail (g); 7=mean thickness of XU (cm) 8=area excavated (m²) 9=mussel shell (g); 10=burnt earth (g); 11=flaked stone artefacts (#); 12=flaked stone artefacts (g); 13=feathers (#); 14=crustacean (g); 15=ochre (g) (XU25=2 pieces, XU27=1 piece); 16=burnt egg shell (g); 17=burnt egg shell (#); 18=unburnt egg shell (g); 19=unburnt egg shell (#); 20=seeds (#); 21=burnt stone (g); 22=leaves (#); 23=bone points (#); 24=wooden digging sticks (#); 25=sheets of cut bark (#); 26=grinding stones (#); 27=grinding stones (g); 28=pandanus nuts (#).

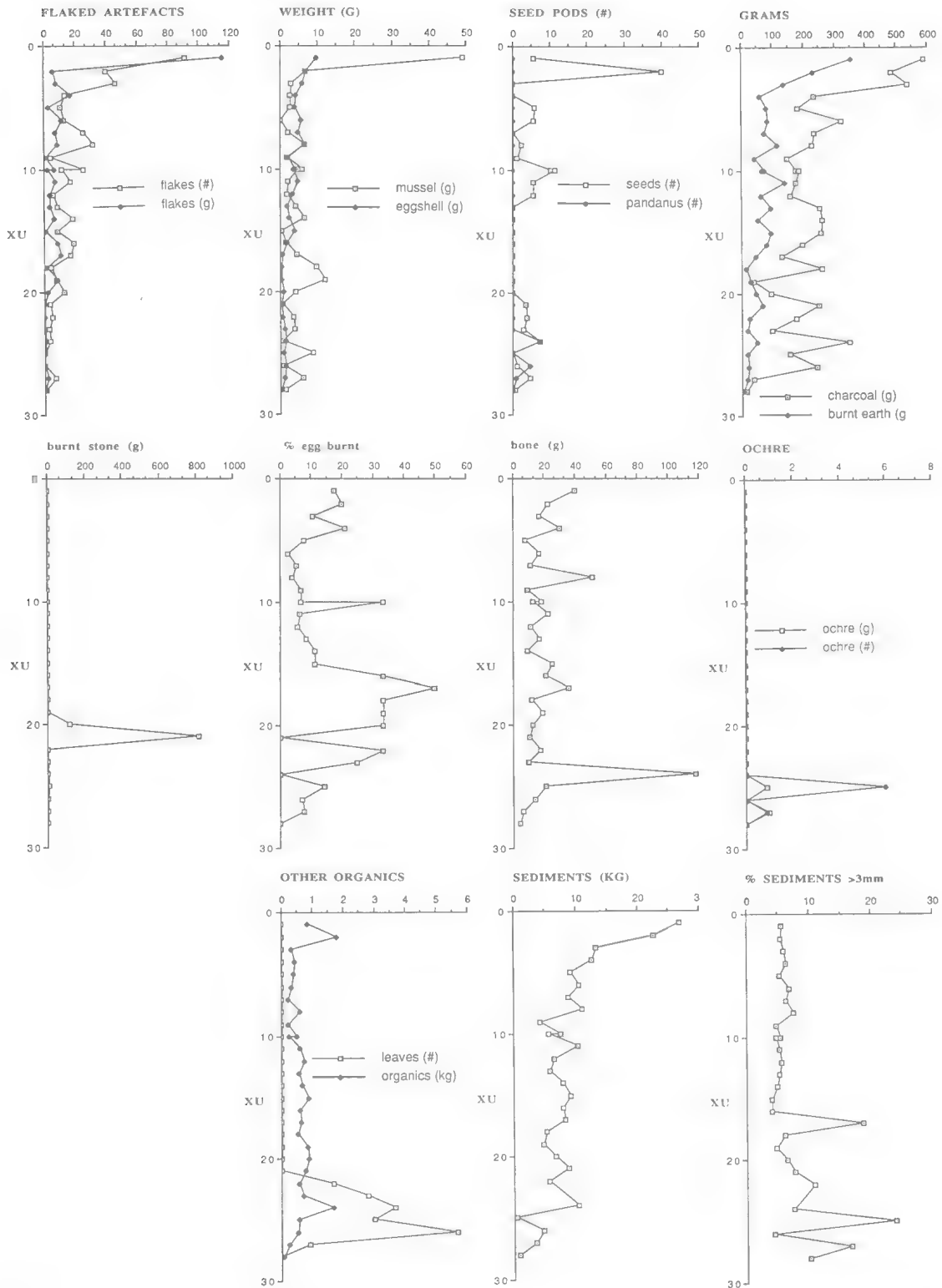


FIG. 10. Mordor Cave, Square H10, deposition rates (per m²/cm of deposit) and proportions of burnt eggshell.

TABLE 8. Mordor Cave, Square H10: deposition rates (per m² per cm of deposit), and proportions of burnt eggshell.

XU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	26.9	5.6	9.7	588.6	353.1	91.4	115.4					49.1	847	697	9.7	17.6	5.7	40.0						
2	22.7	5.4	13.3	485.3	230.7	40.0	5.3					6.7	1804	747	6.7	20.0	40.0	22.7						
3	13.3	5.9	10.7	536.8	135.8	46.3	7.4					3.0	333	448	5.9	10.7		17.1						
4	12.7	6.3	8.7	235.8	60.9	13.3	16.7					2.7	419	362	4.2	21.1		30.0						
5	9.2	5.2	4.2	184.0	78.7	10.4	2.5					2.5	379	292	3.9	7.7	5.9	7.9						
6	10.5	6.8	8.7	322.8	83.6	12.4	10.9						303	356	5.7	2.4	5.5	16.6	1.4					
7	8.8	6.4	5.0	235.8	74.8	25.0	6.8		2.6			2.0	223	291	4.6	5.4		11.3						
8	11.1	7.5	9.4	227.5	117.4	31.4	8.7					6.3	582	374	6.3	3.8	2.4	51.0						
9	4.2	4.7	4.3	147.0	43.0	3.9	0.4					1.7	205	147	2.0	6.7	1.3	9.3						
10a/b	7.6	5.4	6.8	173.8	75.1	25.2	6.3					5.8	476	232	3.8	6.7	10.1	17.9						
10c	5.7	4.7	1.2	185.1	67.8	11.5	2.3					4.6	245	161	3.5	33.3	11.5	12.6						
11	10.3	5.2	10.0	174.0	140.0	17.1	6.9					2.0	609	294	4.6	6.3	5.7	22.3						
12	6.5	5.6	2.2	158.0	61.5	5.6	3.3					1.9	723	180	3.3	5.6	5.6	11.1						
13	5.8	5.3	1.8	253.6	93.9	8.3	3.8					4.0	545	137	1.8	8.3		16.5						
14	7.9	5.0	3.4	260.5	51.6	18.4	6.1					6.3	680	150	2.4	11.1		9.2						
15	9.1	4.0	3.3	257.2	94.7	8.2	0.4					0.4	878	128	3.7	11.1		25.1						
16	7.9	4.1	10.8	196.2	79.0	19.0	8.6					1.6	603	114	1.9	33.3		21.0						
17	8.3	18.8	4.7	130.7	45.9	16.5	10.2					4.3	623	52	0.5	50.0		35.5						
18	5.3	6.1	12.6	258.5	13.9	4.3	1.3					9.6	534	36	0.3	33.3		11.8						
19	4.8	4.7	13.0	40.2	29.1	7.9	8.7					11.9	843	45	0.4	33.3		18.8						
20	6.7	6.5	8.9	94.9	47.0	12.7	2.2		117.1			4.1	882	102	1.0	33.3		12.4						
21	8.8	7.8	8.8	247.6	68.0	3.4	0.3		811.6			0.7	762	37	0.3	0.0	3.4	10.5						
22	5.7	10.9	6.4	177.4	24.6	5.2	0.2					3.5	569	63	0.5	33.3	3.5	17.2		1.7	1.7			
23	?	?	1.1	99.4	17.0	2.9	0.3					3.7	697	55	1.2	25.0	2.9	9.5		2.8		0.1		
24	10.3	7.5	2.6	347.6	49.1	3.7	0.4					0.7	1672	37	1.5	0.0	7.3	117.6		3.7		2.2	7.3	
25	0.3	24.1	14.0	153.6	17.6				8.6	6.0	0.9	8.9	548	15	1.0	14.3		21.1		3.0				3.0
26	4.7	4.3	3.3	241.3	20.7			1.1				0.8	518	69	1.6	7.1	1.1	14.0		5.7		0.2	4.6	
27	3.5	16.9	7.6	37.5	17.9	7.3	1.8			0.9	1.0	6.0	258	42	1.2	7.7	4.6	6.0		0.9			0.9	
28	0.9	10.1	0.5	13.2	5.3	0.7	0.2					1.4	76	15	0.4	0.0	0.7	4.3						

1=sediments excavated (kg); 2=% sediments 3mm; 3=land snail (g); 4=charcoal (g); 5=burnt earth (g); 6=flaked stone artefacts (#); 7=flaked stone; artefacts (g); 8=grinding stones (#); 9=burnt stone (g); 10=ochre (#); 11=ochre (g); 12=mussel shell (g); 13=other organics (g); 14=egg shell (#); 15=egg shell (g); 16=% egg shell burnt (by weight); 17=seeds (#); 18=bone (g); 19=feathers (#); 20=leaves (#); 21=wooden digging sticks (#); 22=crustacean (g); 23=pandanus nuts (#); 24=sheets of cut bark (#).

with thirteen figurative paintings, one track painting, two non-figurative peckings and 812 abraded grooves (including twelve tridents) being determined (Figs 14,15). In addition, numerous weathered peckings are evident subimposed under a series of paintings, but their quantification and precise identification could not be determined due to their advanced stage of deterioration.

Hearth Cave was chosen for excavation because of the presence of patinated peckings at the site. Non-figurative peckings similar to those found at Hearth Cave are relatively rare in the Mitchell-Palmer region, and were believed to have considerable antiquity at the Early Man site near Laura (Rosenfeld et al., 1981). Consequently, a deep sequence was anticipated from

Hearth Cave. Furthermore given that paintings occur in superimposition over the peckings, the recovery of localised in situ ochre should reveal both the antiquity of the paintings and a minimum date for the peckings at the site.

Excavation, Stratigraphy and Dating

Four juxtaposed 50cm × 50cm test pits were excavated, two of which were located against the cave wall in order to determine whether or not rock art continued below the shelter floor (Fig. 16). Only one square (Test Pit 3), however, has been fully sorted and analysed, and consequently this report does not deal with data excavated from the other three squares. It is notable that preliminary analysis of the excavated material from the



FIG. 11. Mordor Cave, large piece of cut bark excavated from XU25, Square H10.

other three squares is consistent with temporal trends observed from Test Pit 3.

Test Pit 3 revealed five stratigraphic units, the first four of which were identified during the course of the excavation (Fig. 17). SU5, the basal layer, is indistinct and was only identified whilst section-drawings were being undertaken, after the excavation was completed. The layers are described in Table 10.

Radiocarbon Dates

Four radiocarbon dates were obtained, two of which come from Test Pit 3, the other two from Test Pit 2: 2360 ± 70 BP (Wk-1716), on charcoal collected from the sieves from an excavation unit located 18.9 to 22.0cm below the ground surface. $\delta^{13}\text{C} = -26.5\text{‰}$. This date comes from near the top of SU3 in Test Pit 2; 3494 ± 84 BP (R 14023 NZA 1383). This is an AMS date obtained on charcoal from the sieves, located 36.4 to 40.0cm below the ground surface. It was obtained from slightly below the surface of SU4b in Test Pit 2. $\delta^{13}\text{C} = -25.9\text{‰}$; 4100 ± 120 (Beta-54024), obtained on



FIG. 13. Mordor Cave, feather excavated from XU3, Square H10 (scale in 2mm units).

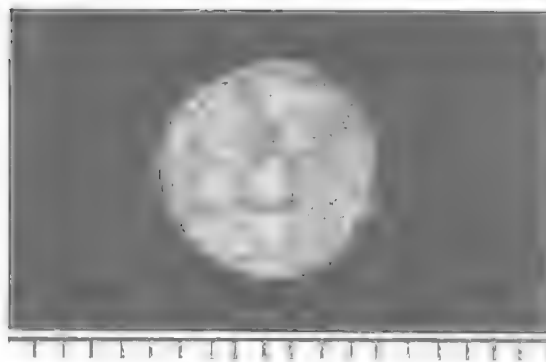


FIG. 12. Mordor Cave, fig excavated from XU23, Square H10 (scale in 2mm units).

charcoal collected from the sieves. It dates excavation unit 14a (SU4b), located in Test Pit 3, 40.6 to 45.7cm below the ground surface; $21,500 \pm 250$ (Wk-1719), a radiocarbon date obtained from land snails (*Xanthomelon* sp.) located 51.4 to 57.1cm below the ground surface (XU16a). It dates the SU4b-SU5 interface (Test Pit 3). $\delta^{13}\text{C} = -7.2\text{‰}$.

Cultural Materials

Unfortunately it is not possible to determine deposition rates for the earliest times represented by the Hearth Cave excavations, as radiocarbon dates are not available for the basal units. By assuming a *minimum* of 21,500 years of occupation, however, *maximum* deposition rates can be calculated for the earliest occupational deposits, and temporal patterns can then be explored. It is stressed, however, that the calculation of such rates are for heuristic purposes only. They are employed to determine temporal trends rather than absolute, synchronic values.

Given the uneven nature of the stratigraphic

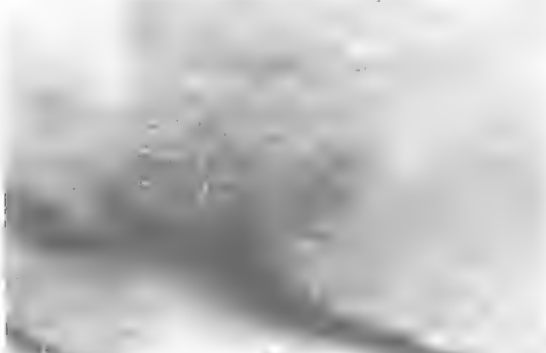


FIG. 14. Hearth Cave, rock wall showing evidence of very weathered peckings and paintings.

TABLE 9. Mordor Cave faunal remains: Minimum Numbers of Individuals (MNI), Square H10 (after Dagg, 1992). Question marks indicate the presence of identified species which are believed to be post-depositional intrusions into that unit (for reasons outlined in Dagg, 1992). P=present.

Species	SU1	SU3	SU3/4	SU4	SU4/4F	SU4/4H	SU4H	Total
<i>Macropus robustus</i>	0	0	0	0	0	0	1	1
<i>Macropus agilis</i>	0	2	0	2	0	0	1	5
<i>Petrogale</i> sp.	0	1	?	3	0	0	3	7
<i>Pseudocheirus peregrinus</i>	1	?	0	0	0	0	0	1
<i>Trichosurus vulpecula</i>	1	0	0	1	0	0	0	2
Peramelidae	0	1	0	2	0	0	0	3
Dasyuridae	0	1	0	0	0	0	0	1
<i>Uramys caudimaculatus</i>	0	0	0	2	0	0	0	2
Other Muridae	1	1	0	6	1	0	2	11
<i>Canis familiaris</i>	0	1	0	0	0	0	0	1
<i>Varanus</i> sp.	0	0	0	1	0	0	0	1
Agamidae	0	1	0	?	0	1	1	3
Scincidae	1	1	0	1	0	0	1	4
Boidae	1	0	0	1	0	0	0	2
Elapidae	0	1	0	0	0	0	0	1
Teleostomi	1	0	0	0	0	0	1	2
<i>Velesunio</i> sp.	P	P	P	P	P	P	P	
Crab	0	0	0	0	0	?	1	1
<i>Xanthomelon</i> sp.	P	P	P	P	P	P	P	
<i>Alectura lathami</i> egg	P	P	P	P	P	P	P	
<i>Alectura lathami</i>	0	1	0	0	0	0	0	1

units near the southern end of the square, especially where SU2 dips down to form a depression, the calculation of deposition rates was only attempted for those parts of the pit where strata are laid approximately horizontally. Table 11 presents the raw data excavated from Test Pit 3, whilst Table 12 transforms this data to deposition rates for each spit (excavation unit). In Table 13, a similar procedure is attempted for each stratigraphic unit.

Although occupation at Hearth Cave began

sometime before 21,500±250BP, sedimentation rates peaked between approximately 3500BP and 2500BP, after which they again decreased. Deposition rates of all cultural materials show a similar pattern, being low until approximately 3500BP, and subsequently increasing until 2500-2000BP, after which they decreased slightly and remained relatively stable from then on (Tables 11,12, Fig. 18).

The Hearth Cave bone has not yet been identified to species, but it is notable that very large

TABLE 10. Stratigraphic Units (SUs) from Hearth Cave, Test Pit 3.

SU Description

- 1 The surface layer, consisting of loose, ashy sediments containing leaves, twigs and cultural materials.
- 2 Similar to SU1, but sediments are more compact. Charcoal and mussel shell are very abundant, especially immediately above SU3. Sediments are ashy silts. Unlike SU1, there are virtually no leaves or twigs in SU2. The boundary with SU1 above is marked. Towards the southern parts of the excavation, SU2 dips down, forming a depression where charcoal, burnt earth and mussel shell are particularly abundant. It is possible, but not certain, that this depression represents a hearth.
- 3 Extremely gravelly layer, whose boundary with SU2 above is distinct. Given the coarseness of sediments in SU3, it is thus possible that this layer represents a lag or deflated deposit. This is supported by the considerably larger mean weight of stone artefacts excavated from SU3 than from the other SUs, implying that fine sediments (including very small stone artefacts) have been washed away. Given that deposition rates of cultural materials peak during SU3 times, this may indicate that their original densities should in reality be even greater. Rootlets are common at the interface between SU2 and SU3. Cultural materials were identified in situ throughout SU3.
- 4a Silty clay containing very large numbers of land snails (especially *Xanthomelon* sp.). Some gravel is present, but in significantly smaller numbers than in SU3 above. SU4a is localised within Test Pit 2 only, and does not appear in Test Pit 3.
- 4b SU4b consists of silty clays containing cultural materials. Some very fine gravel occurs, but as was the case with SU4a, they are not as numerous as in SU3.
- 5 Humid clay containing numerous small calcium carbonate concretions. Although SU5 continues beyond the base of the pit, excavation was stopped because no cultural materials were noted in situ within this layer. Subsequent analysis of materials in the laboratory, however, proved that SU5 is not culturally sterile, and investigations will therefore be resumed at a later date to determine the nature of early deposits at Hearth Cave. The fact that basal occupation was not reached does not, however, affect the thrust of this paper, nor the conclusions reached here.

TABLE 11. Hearth Cave: list of materials excavated and information on sediments.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	1	44	39.6	129.4	161.1	3.3	4.4	26.3		12.5	41	31.0		9.5	6	4	5.9	2750	4.9	0	1.6	1.6	0.84
2	1	106	33.8	179.0	223.1	9.6	10.1	63.1		44.8	53	12.6	1	19.0	8.75	10	11.3	2750	2.8	1.6	4.9	3.3	0.32
3	1	47	34.4	53.1	13.3	3.8	1.2	28.8	40.4	22.3	24	7.0		2.3	9	5	4.7	2750	0.4	4.9	5.8	0.9	0.73
4	2	102	78.5	109.4	32.8	9.1	9.5	42.5		46.6	71	20.7		7.0	9	10	11.6	2700	1.2	5.8	9.2	3.4	0.77
5	2	119	55.6	131.7	19.4	13.1	2.6	9.4	68.4	47.0	80	92.9	1	27.4	8.5	12	12.4	2700	0.7	9.2	12.4	3.3	0.47
6	2	90	25.2	105.1	36.1	12.7	5.5	22.7		43.7	71	31.6		19.0	8.5	11	11.6	2700	1.0	12.4	15.1	2.7	0.29
7	2	104	30.5	69.0	15.0	10.3	1.3	5.2		45.6	39	8.7	3	21.8	8.5	1	11.0	2650	0.8	15.1	17.7	2.5	0.24
8b	2	13	0.8	3.6	2.5	3.0	0.4	0.5		7.8	7	0.4		2.0	8.5	5	5.3	1160	0.2	17.7	22.3	4.1	0.06
10b	2	56	10.4	35.3	67.2	7.1	1.3	7.0		16.3	22	4.4		5.4	8.5	10	10.2	1900	1.3	22.3	25.9	3.6	0.19
11b	2	30	4.4	5.6	14.4	4.4	0.4	0.2		8.1	3	0.1		1.5	8.5	6	6.0	1350	0.2	25.9	29.7	3.8	0.15
12b	2	24	4.6	8.8	43.7	6.3	0.5	0.1		8.5	16	1.3		12.2	8.5	10	11.0	1300	0.3	29.7	36.1	6.4	0.19
13b	2	21	3.0	8.9	30.7	2.3	0.1	0.1		1.6	2	0.4		3.1	8.5	6	6.6	820	0.2	36.1	40.4	4.3	0.14
14b	2	12	1.9	9.9	62.3	1.5	0.1	0.1		1.2	3	0.7		1.8	8.5	4	6.8	750	0.2	40.4	44.5	5.1	0.16
15b	2	14	2.0	5.1	33.4	1.0	0.1			0.5				5.8	8.5	5	4.5	470	0.1	44.5	50.3	4.8	0.14
16b	2	6	0.2	1.2	51.6	0.8	0.1			0.4	2	0.1		0.2	8	5	5.7	330	0.1	50.3	57.4	6.9	0.03
8a	2/3	78	25.8	37.5	52.4	4.6	0.9	4.7		26.4	26	6.1		1.4	8.5	5	4.7	1550	0.6	17.7	18.5	1.3	0.33
9	3	72	44.4	137.1	283.9	3.3	0.6	4.7		1.9	31	24.9		1.9	8	6	6.4	810	2.6	18.5	21.6	3.2	0.62
11a	3	17	47.9	102.6	377.0	1.2	0.7	1.1		3.3	16	8.6		1.2	8.5	4	5.8	850	1.8	21.6	25.3	3.7	2.82
11a	3	40	90.3	189.5	647.1	2.2	1.3	16.1		8.8	66	80.2		1.3	8.5	8	10.9	1500	1.9	25.3	29.8	4.5	1.84
12a	3	30	80.1	143.9	631.6	2.9	1.9	2.9		4.9	28	25.0		1.5	8.5	8	9.9	950	2.6	29.8	36.5	8.1	2.67
12c	3/4b	19	6.8	65.4	294.4	2.8	1.3	0.8		4.6	17	9.6		3.3	8.5	5	5.8	450	1.0	29.8	36.9	7.1	0.36
13a	4/4b	25	18.7	65.2	63.1	1.9	2.1	0.5		4.1	24	8.0		2.4	8.75	?	9.8	1800	1.5	37.3	40.6	3.3	0.75
14a	4b	3	0.1	17.9	414.4	1.3	0.1	0.4		1.1	2	0.2		0.6	9	8	9.7	1950	1.0	40.6	45.7	5.1	0.63
15a	4b/5	5	0.2	15.9	213.9	1.2	0.2	0.1		1.1	3	0.1		1.7	8.25	11	13.5	2200	1.2	45.7	51.4	5.7	0.64
16a	4b/5	38	3.5	16.8	151.2	0.7	0.1	2.2		0.2	2	1.1		0.4	8.5	12	15.4	2150	1.1	51.4	57.1	5.7	0.89
17	4b/5	2	0.1	1.7	78.7	0.2	0.1			0.1	4	0.1		0.7	8.25	12	14.0	2750	1.2	56.7	61.5	4.7	1.05
18	5	12	0.5	4.2	41.9	0.6	0.2			0.1	3	1.7		4.1	8.5	14	16.9	2750	2.1	61.5	66.6	5.1	1.04
19	5	6	0.2	0.8	36.6	0.1				0.1	8	2.4		2.4	8.25	7	11.7	1250	1.3	66.6	72.9	7.9	0.63
20	5	5	0.2	1.8	2.4	0.1	0.1				7	0.5		0.1	8.25	7	8.2	1250	0.8	72.9	78.2	5.4	0.04
21	5			0.2	0.1						1	0.1		0.1	8.25	?	3.7	625	0.6	78.2	83.4	5.2	

1=stone artefacts (#); 2=stone artefacts (g); 3=bone (g); 4=land snail (g); 5=egg shell (g); 6=mussel shell (g); 7=burnt earth (g); 8=burnt stone (g); 9=charcoal (g); 10=ochre (#); 11=ochre (g); 12=bone points (g); 13=other organics (g); 14=pH; 15=volume (litres) dug; 16=weight (kg) dug; 17=area (cm²) dug; 18=residue >3mm (kg); 19=mean start depth below surface (cm); 20=mean end depth below surface (cm); 21=mean thickness of XU (cm); 22=mean weight of stone artefacts (g).

numbers of Brush Turkey egg shell occur in all cultural layers. Brush Turkeys lay their eggs from the end of the dry to the beginnings of the wet season (August-December), offering a reliable seasonal marker for when the site was used (W. Longmore, pers. comm., 1992). Although this question needs further attention, it is possible that the repeated high numbers of egg shell at Hearth Cave implies great continuity of a seasonal settlement system whereby rockshelters from the region were repeatedly occupied during the wet season. This does not deny the possibility, however, that the site was also used during other times of the year. Further research into this issue will have to await systematic investigation of the faunal material from Hearth Cave and elsewhere, as well as investigations in other sites from the region (including both rockshelter and open sites).

The stone artefacts are largely 'amorphous', although technologically they may possess highly diagnostic characteristics (this remains to

be investigated). Only two formal stone tool 'types' were identified from the excavation: a fragment of 'edge-ground axe' from XU5 (1100-1450BP), and a 'burren adze slug' from XU4 (700-1100BP). Given their low numbers, however, it is difficult to make any generalisation about typological change in the stone tool assemblage from the site. It may nevertheless be significant to note that the 'burren adze' found at Hearth Cave was dated to around the same time as their appearance in other sites excavated from south-east Cape York Peninsula (David, in prep.).

The temporal distribution of in situ ochre is similar to the distribution of other types of cultural items. Numbers of ochre fragments peak during the last 3500 years, and high levels are maintained until ethnohistoric times. The very low ochre deposition rates before approximately 3500BP are likely to signify that the cave paintings currently visible at the site post-date this time, although the excavations have furnished no



FIG. 15. Hearth Cave, freehand recording of part of the main painted and pecked panel. Not to scale.

direct indication of the age(s) of the underlying – and therefore older – peckings.

The increases in deposition rates documented from Hearth Cave after 3500BP include the following: 1, Increased sedimentation rates, which Hughes (1977) and Hughes & Lampert (1982) have argued may be related to increases in occupational intensities; 2, Increases in the deposition rates of bone, charcoal and burnt earth, which together may imply increased rates of hearth establishment and firing activity, and increases in the amounts of food consumed and discarded at the site; and 3, Increases in ochre, which implies an increase in painting activity.

It is, nevertheless, difficult to determine further the exact characteristics of the temporal frameworks involved. This is due to an absence of fine stratigraphy at the site, making it difficult to obtain discrete temporal units which can then be used to construct a chronological framework.



FIG. 16. Hearth Cave, the excavation pit, showing the west section (scale in 5cm units).

Consequently, we have resorted to the use of a depth-age curve to calculate temporal trends. Furthermore, the availability of three dates from 2360 ± 70 to 4100 ± 120 BP has enabled a fairly good assessment of changes around this time.

DISCUSSION

The distribution of in situ ochres at Mordor Cave and Hearth Cave is comparable to their distributions in other excavated sites from south-east Cape York Peninsula. In all sites, peak ochre deposition rates occur late in the sequence and continue to increase until very recent times. This is the case for the following:

- 1, the Early Man rockshelter, where in situ ochres increase significantly after either 5000BP or during the last two millennia or so (the precise dating is debatable because of chrono-stratigraphic uncertainties) (Rosenfeld et al., 1981; David, 1991b);
- 2, Green Ant Rockshelter (Koolburra Plateau), where they increase dramatically after 2500BP (Flood & Horsfall, 1986; Flood pers. comm., 1991);
- 3, Mitchell River Cave (Mitchell River), where the only fragment of ochre was obtained from deposits dating to the last 1000 years (David, 1991a);
- 4, Echidna's Rest (Chillagoe), where ochre deposition rates double after 3000 years ago, and continue to increase during the last 700 years (David, 1990).

The implications of this are that cave paintings in southeast Cape York Peninsula pertain particularly to the mid to late Holocene. Painting conventions vary greatly across space throughout southeast Cape York Peninsula, indicating a highly regionalised social landscape during this

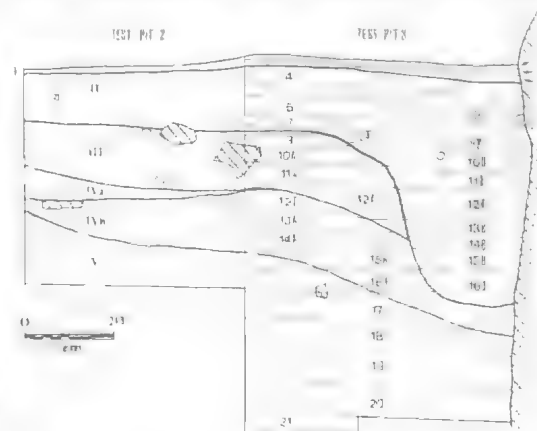


FIG. 17. Hearth Cave, stratigraphy, east section.

TABLE 12. Hearth Cave: deposition rates by XU (per m² per 100 years). Note that rates could not be calculated for XUs below XU15a, as no radiocarbon determinations were obtained from the lower XUs.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12
1	1	200	80.0	67.1	74.5	56.4	235.3	8.0	6.0	22.7	47.8		0.9
2	1	600	96.4	30.7	48.2	11.5	162.7	9.2	8.7	40.7	57.4		0.9
3	1	700	170.9	125.1	87.3	25.5	193.1	4.4	13.8	81.1	164.7	146.9	6.4
4	2	1100	94.4	72.7	65.7	19.2	101.3	8.8	8.4	43.0	39.4		0.9
5	2	1450	125.9	58.8	84.7	98.3	139.4	2.8	13.9	49.7	9.9	72.4	0.9
6	2	1800	95.2	27.4	75.1	33.4	111.2	5.8	13.4	52.6	24.0		0.9
7	2	2100	130.8	37.7	49.1	10.9	86.8	1.6	13.0	57.4	6.5		0.9
8a	2/3	2150	1006.5	232.2	335.5	78.7	483.9	11.6	59.4	340.6	63.2		0.9
9	3	2500	254.0	156.6	109.3	87.8	483.2	2.1	11.6	38.4	16.6		0.9
10a	3	2700	100.0	281.8	94.1	50.6	603.5	4.1	7.1	19.4	6.5		1.9
11a	3	3000	108.9	206.7	133.3	178.2	421.1	2.9	4.9	19.6	35.8		1.5
12a+c	3/4b	3500	20.0	124.1	64.3	49.4	299.0	4.6	8.1	13.6	5.3		1.5
13a	3/4b	3850	38.0	28.4	36.5	12.2	99.1	3.2	2.9	6.2	6.8		0.9
14a	4b	8250	0.3	<0.1	0.2	<0.1	2.1	<0.1	0.2	0.1	<0.1		0.1
15a	4b/5	17450	0.2	<0.1	0.1	<0.1	0.8	<0.1	0.1	0.1	<0.1		0.1

1=end years BP for spit 2=stone artefacts (#); 3=stone artefacts (g); 4=ochre (#); 5=ochre (g); 6=bone (g); 7=mussel shell (g); 8=egg shell (g); 9=charcoal (g); 10=burnt earth (g); 11=burnt stone (g); 12=sedimentation (cm).

time (e.g. Rosenfeld, 1982, 1984; David & David, 1988). Considerable support for these findings have been obtained for very recent times from the ethnographic record. More problematic is an apparent, more homogeneous engraving tradition characterised by non-figurative and animal track peckings throughout the region (see Maynard, 1977, 1979). Their probable greater antiquity and relative homogeneity may imply that inter-regional networks were structured differently during earlier times (before the mid Holocene?), although this issue needs to be further investigated by obtaining more secure dates on the engravings themselves. Nevertheless, the repeated occurrence of engravings *underneath* paintings at Laura, the Koolburra Plateau, Chillagoe and elsewhere, indicates that this temporal pattern has so far withstood the test of time (cf. Flood, 1987; Rosenfeld et al., 1981; Woolston & Trezise, 1969). The conclusion that the last few thousand years of prehistory in southeast Cape York Peninsula witnessed a fundamental restructuring of artistic, and therefore probably also socio-cultural, networks appears to be strengthened with every excavation adding further support for a largely late Holocene antiquity of cave paintings. The highly regionalised nature of these paintings contrasts markedly with the relatively homogeneous nature of the preceding engravings.

Related to this question, it is noted that a significant proportion of the excavated faunal remains from Mordor Cave consist of food debris dominated by macropods — *Petrogale* sp., *Macropus agilis* and *Macropus robustus* — and other marsupials (e.g. *Trichosurus vulpecula*).

The total absence of macropods from the paintings, and the general non-conformity between the range and relative representation of fauna recovered from the excavations and those represented in the paintings may be of great interest. The implications are that the animals painted on cave walls during the mid to late Holocene are not simply a reflection of dietary breadth, nor simply an indication of the symbolic importance of the hunted and foraged fauna. On the contrary, the two sources of faunal representation — the painted animals and the animals represented in the food debris — represent two distinct information domains, each of which relates to a different set of socio-cultural principals (set within a socio-cultural system or systems). In other words, data obtained from the excavated food remains relates specifically to subsistence behaviour, whereas the painted forms are an archaeological window into a totally different aspect of prehistoric life within a site and region. By investigating the latter we are investigating a system of visual forms structured by socio-cultural convention, a system of symbols whose investigation can reveal something about the nature of symbolic vocabularies but not about their related original meaning contents (cf. Frost et al., 1992). Although rock art has largely been ignored in Australian archaeology until recent times, it is important to note that once different bodies of rock art from a single region (and across space) are dated, continuities and discontinuities in visual conventions can be investigated. This does not require the art having had 'meaning' to its creator in the sense that it was created for a particular reason beyond 'art for art's

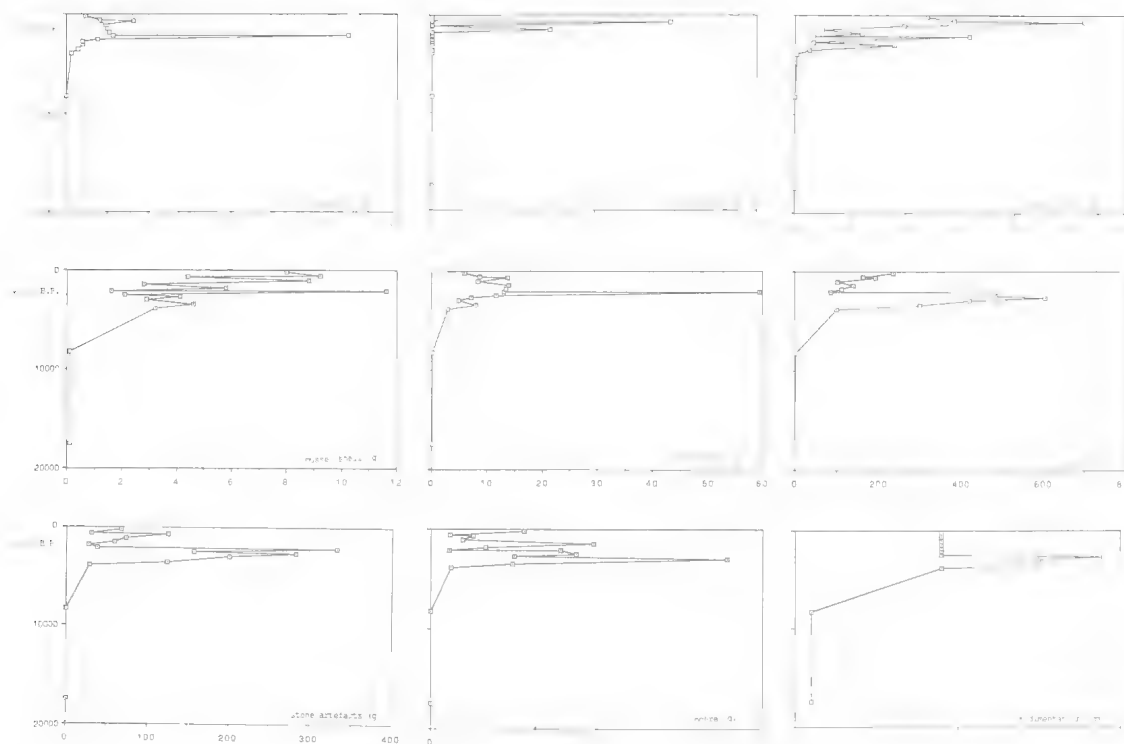


FIG. 18. Hearsh Cave, deposition rates by XU (per m²/100 years). Rates for SU5 are maximum rates only, based on the assumption that cultural deposits began 21,500BP. In reality, this is only a minimum date for occupation. Therefore, the temporal trends evident in the curves would be accentuated with longer occupation at the site.

sake', for what is at stake concerns the structuring of socio-cultural imagery, of the ordering of symbols as formal representations and of the portrayal of rock art forms in specific proportions. For example, why are there no recorded macropods in the Mitchell-Palmer rock paintings, especially given their importance in the rock art of Laura to the immediate north? Why does the nature of painted representations change less than 50km to the south of the Mitchell-Palmer region, from a predominantly figurative painting region to a

non-figurative one? The implications are that during relatively recent times at least, spatial discontinuities existed in the distribution of socio-cultural conventions relating to rock art through space (David, in prep.). Given that rock art does not necessarily relate to any specific aspect of social life such as subsistence, however, it does not necessarily follow that the documented discontinuities in rock art also represent differences in other social practices. But the regionalised nature of rock art traditions during the late

TABLE 13. Hearsh Cave: deposition rates by SU (per m² per 100 years). Note that some XUs are interface spits, and therefore their relative contributions to the various SUs to which they belong have been taken into account in the calculations presented.

SU	XUs	1	2	3	4	5	6	7	8	9	10	11	12
1	1-3	700	102.3	54.6	61.3	26.2	187.7	8.2	8.7	41.4	61.3	21.0	206.5
2	4-8a	2150	242.2	61.4	104.7	42.0	146.5	6.4	26.8	66.0	22.9	17.5	237.5
3	8a-13a	3450	195.2	210.7	128.2	103.9	516.0	5.1	12.0	33.2	17.6		1731.6
4b	12c-17	99000	12.0	2.4	6.2	2.4	19.2	0.4	0.9	1.3	0.3		117.4
5	15a-21	>21,500	<1.8	<0.1	<1.3	<0.3	<0.9	<0.1	<0.1	<0.1	<0.1		<11.3

1=end years BP 2=stone artefacts (#); 3=stone artefacts (g); 4=ochre (#); 5=ochre (g); 6=bone (g); 7=mussel shell (g); 8=egg shell (g); 9=charcoal (g); 10=burnt earth (g); 11=burnt stone (g); 12= land snail (g).

Holocene implies regionalised symbolic behaviour throughout southeast Cape York Peninsula during that time. The precise nature of this regionalisation — whether it involved broader discontinuities or not — remains unknown. It is therefore to explore such issues that we present this paper, for it is by generating systematic research on past socio-cultural systems in southeast Cape York Peninsula — that is, on the relationship between resource structures, symbolic representations, technological conventions etc., and their continuities and discontinuities across space and through time — that significant new inroads will be made in Aboriginal prehistory.

ACKNOWLEDGEMENTS

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A NEW SPECIES OF *LYGISAURUS* DE VIS (REPTILIA: SCINCIDAE) FROM
MIDEASTERN QUEENSLAND

PATRICK J. COUPER

Couper, P.J. 1993 06 30; A new species of *Lygisaurus* de Vis (Reptilia: Scincidae) from mideastern Queensland. *Memoirs of the Queensland Museum* 33(1): 163-166. Brisbane. ISSN 0079-8835.

Lygisaurus zuma sp.nov. is from open forests and riparian habitats of the Mackay district, mideastern Queensland. It is distinguished from its congeners by the following combination of characters: midbody scale count 23-24, supraciliaries usually 6, ear lobules flat and low, and palpebral disc large. Faecal analysis shows that this species feeds on small arthropods. In captivity, male *L. zuma* display territorial behaviour and both sexes give a brief, head-bobbing display when establishing themselves in a sunning position. Male *L. zuma* develop a red breeding flush on their throats and tails, which reaches full intensity by late October. A captive female produced two soft-shelled, oval shaped eggs, in mid-November.

□ *Lygisaurus zuma*, Scincidae, new species, open forest, Queensland.

Patrick J. Couper, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 5 January, 1993.

Ingram and Covacevich (1988) resurrected the genus *Lygisaurus* from the synonymy of *Carlia* to accommodate the small, brown litter-dwelling skinks, which had formed a discrete unit within *Carlia*. They transferred four species (*L. foliorum*, *L. aeratus*, *L. laevis* and *L. macfarlandi*) to *Lygisaurus* and described three new species (*L. rococo*, *L. sesbrauna* and *L. tanneri*) from north-eastern Queensland. In addition, *Menetia timlowi* (Ingram, 1977) was reallocated to the genus *Ly-*

gisaurus. Subsequently, Greer (1991) changed the generic diagnoses of *Lygisaurus* and *Menetia* and concluded that *L. timlowi* was more closely related to *Menetia* than to *Lygisaurus*. He reasigned it accordingly.

During recent field surveys north of Mackay, mideastern Queensland, a new *Lygisaurus* closely resembling *L. tanneri* was collected. The new species conforms to the generic diagnoses of Ingram and Covacevich (1988) and Greer (1991). On external features alone, it is readily referable to the genus *Lygisaurus* by the presence of ear lobules, which *Menetia* lacks (Greer, 1991). Further, the number of paravertebral scales in the new species (44-48) is within the range of *Lygisaurus* (39-50), whereas *Menetia* has 52-66 (Greer, 1991). The discovery of a new species of *Lygisaurus*, following a recent revision of this genus, emphasises the importance of field surveys in areas that have been previously overlooked. With the exception of the Eungella rainforest block, the forests of the Mackay area have been largely ignored because researchers have focused their attention on forests further north.

Body measurements and morphological characters follow Ingram and Covacevich (1988). SV = snout-vent length; HW = head width; TL = tail length; HL = hindlimb length. The number of supraciliaries, supraoculars, ear lobules, supralabials and subdigital lamellae have been recorded from both sides of the body. The subdigital lamellae count includes the most distal scale. In addition, the numbers of enlarged nuchal scales and paravertebrals have also been counted

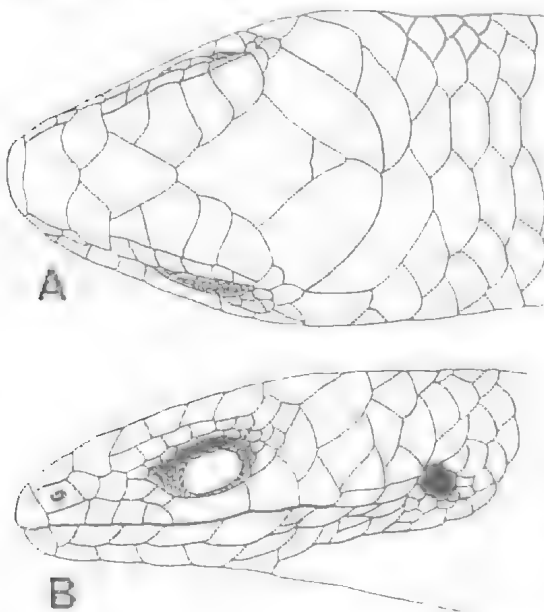


FIG. 1. *Lygisaurus zuma* (J55760). A, Dorsal view of head. B, Lateral view of head.



FIG. 2. *Lygisaurus zuma* (J56874) Boulder Ck, MEQ (S. Wilson).

(sensu Greer, 1991). All specimens examined are in the Queensland Museum.

***Lygisaurus zuma* sp.nov.**
(Figs 1-4)

MATERIAL EXAMINED

HOLOTYPE: J55760 female, Boulder Ck, via Mt Charlton, MEQ (21°01'S, 148°43'E), collected by P.J. & K.L.D. Couper on 21-23 July 1992.

PARATYPES: J53397, J55761-7, J56874-6, J56883 Boulder Ck, via Mt Charlton, MEQ; J56278, J56280 small knoll immediately WNW of Mt Ossa township, E of where Carey Ck crosses Bruce Highway, MEQ (20°55'S, 148°48'E); J56279 small knoll just east of the Gceberga-Buthurra Rd, 6.7km from where the road meets the Bruce Highway opposite Buthurra, MEQ (21°01'S, 148°48'E); J56765 Neilson Ck, at the base of Mt Blackwood, MEQ (21°01'S, 148°58'E); J56786 proposed Teemburra Ck Dam, near Pinnacle, N of Mackay, MEQ (21°13'S, 148°39'E).

DIAGNOSIS

A medium sized (maximum SV 34mm) *Lygisaurus* (Fig. 2). *L. zuma* sp. nov. has a movable lower eyelid, a character it shares with *L. aeralatus*,

L. laevis, *L. macfarlani*, *L. rococo*, *L. sesbrauna* and *L. tanneri*. *L. zuma* sp. nov. is distinguished from *L. rococo* by midbody scale count (23-24 vs 27-30); from *L. tanneri* by the number of supraciliaries (usually 6 vs usually 7); from *L. aeralatus*, *L. laevis* and *L. sesbrauna* by the nature of the ear lobules (flat and low vs sharp); from *L. macfarlani* by the size of the palpebral disc (large, occupying more than half of the lower eyelid vs small, occupying less than half of the lower eyelid), a character which further distinguishes it from *L. laevis*, *L. sesbrauna* and *L. tanneri*.

DISTRIBUTION

The Mackay district, mideastern Queensland (Fig. 3).

DESCRIPTION

SV: 23-34 (N = 18, mean 30.0). Proportions, (% SV): HW, 12-16 (N = 18, mean 14.3); TL, 130-178 (N = 6, mean 151.4); HL, 28-40 (N = 18, mean 35.7). Supraciliaries 6, rarely 5 or 7 (N = 36, mean 6.0). Palpebral disc large, occupying more than half of the lower eyelid. Lower eyelid movable. Ear aperture much smaller than palpebral disc; varying in shape from round to almost



FIG. 3. Distribution of *Lygisaurus zuma*.

horizontal, with low flat lobules around the margin. Supraoculars 4, rarely 3 ($N = 36$, mean 3.9). Supralabials 7 ($N = 36$), with the fifth under the eye. Three scales between the second presubocular and the nasal scale. Enlarged nuchal scales 2-3 ($N = 18$, mean 2.1), with two contacting the parietal shields. Midbody scale rows 23-24 ($N = 17$, mean 23.7). Number of scales from chin to vent 50-58 ($N = 17$, mean 53.5). Number of paravertebral scales 44-48 ($N = 17$, mean 46.6). Number of lamellae under fourth toe 19-23 ($N = 34$, mean 21.3).

Dorsal colour pattern iridescent grey-brown with longitudinal rows of small black flecks that become more concentrated on the flanks, forming a darker lateral zone. Ventral surface silvery white with a dark edging to the belly scales; chin immaculate. Head coppery with scattered dark blotches. In life, eye pale green with a black pupil. Breeding males have red tails and throats.

ETYMOLOGY

The name is derived from Montezuma II, the last Aztec emperor, who was a sun-worshipper. The name alludes to the lizard's basking habits. The epithet is to be treated as a noun in apposition.

HABITAT

L. zuma lives in the leaf-litter of open forests and associated riparian habitats. J53397, 55760-

55767, 56874-56876, 56883 were collected from a mixed, eucalypt-dominated woodland, predominantly comprised of the following species; *Eucalyptus dolichocarpa*, *E. intermedia*, *Pandanus tectorius*, *Ervatamia orientalis*, *Flindersia schottiana*, *Planchonia careya*, *Acacia flavescens*, *Randia fitzalanii*, *Mallotus philippensis*, *Glochidion sumatranum* and *Lophostemon suaveolens* (Fig. 4). J56279 was collected from a stand of *L. suaveolens* with scattered *Eucalyptus platyphylla* and young *M. philippensis*. J56280 is from an *E. intermedia* dominated forest with an understorey of *Lophostemon confertus*. J56765 was collected from a creek-bed containing riverine vegetation, immediately adjacent to a eucalypt dominated woodland. J56786 was taken from an open riparian forest dominated by *Casuarina* sp. J56278 was found in dense leaf litter in a dry gully in a patch of rainforest.

The penetration of open forest species into rainforest is discussed by Covacevich and McDonald (1991). The occurrence of *L. zuma* in rainforest may be an example of this, probably the result of severe drought. Specimen J56278 was collected during September 1992, one of the driest periods on record for the Mackay area. Field surveys conducted in October 1991 failed to find this species in rainforest, despite a total 18 man-days spent in rainforests around Mt Ossa and Mt Charlton.

HABITS

Like all *Lygisaurus*, *L. zuma* is a small, ground-dwelling diurnal skink. Individuals seen at Boulder Ck during July 1992 were actively foraging through the litter layer from mid-morning to early afternoon. All observed activity was confined to patches of sunlight. Ground temperature in these sun patches ranged from 24-28°C.

An examination of four faecal samples showed that *L. zuma* feeds on small arthropods. One of the samples contained two ground spiders of the families Lycosidae and Pisauridae and another two of the samples each contained a single planthopper (Hemiptera: Fulgoroidea). The fourth sample, while containing no prey items, consisted of numerous scales presumably ingested by the skink while sloughing. Specimens kept in captivity readily eat termites, actively avoiding the soldiers and preferring the larger, more succulent workers.

Male *L. zuma* observed at Boulder Ck during July 1992 had not yet developed their full breeding colours. While the lower labials displayed a well developed, red flush, the scales of the throat

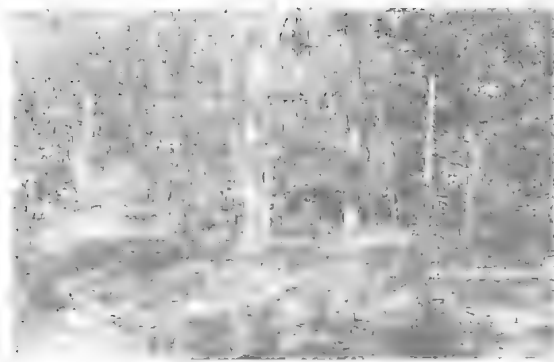


FIG. 4. Open forest habitat of *Lygisaurus zuma*.

remained white with only a hint of orange appearing around the margins. Breeding colours develop to full intensity by late October, as was the case with J53397 and J56765, and begin to fade by early December (captive males J56874 and J56876). In captivity, territorial behaviour was evident in males well before breeding colours had fully developed. The larger of two males sharing an enclosure with two females would actively chase the other male whenever contact occurred. Both males and females gave a brief display of head-bobbing as they first established themselves in a sunning position.

Captive female J56883 (SV: 33.9mm) laid two soft-shelled, oval-shaped eggs on 18 November 1992 (± 2 days). The eggs became desiccated and required rehydrating before any measurements could be taken. Egg length ranged from 7.52–7.54mm egg width from 3.85–3.95mm.

ACKNOWLEDGEMENTS

This work was funded by a grant from the National Rainforest Conservation Programme, administered by the Department of Environment

and Heritage. I am especially grateful to Duncan Limpus for his efforts in obtaining the first specimen of *L. zuma* from our Boulder Ck campsite. I also wish to thank Peta Woodgate and Lynette Dickfos for typing; Glen Ingram, Jeanette Covacevich and Steve Wilson for critically reading the manuscript; Steve Wilson for his excellent photograph; Gray Cranitch for preparing the photographic figures; David Nebauer for preparation of the map; Peter Thompson for identifying botanical specimens; Geoff Monteith and Kevin Lambkin for identifying insect fragments contained in faecal samples; Michael Cunningham, Kate Couper and Alan Beckman for their assistance in the field; Tim Low and Morgan Thomas for collecting additional material; and Lauren Keim for her assistance in the laboratory.

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A NEW SPECIES OF *UPEROLEIA* (ANURA: LEPTODACTYLIDAE:
MYOBATRACHINAE) FROM NORTHEASTERN AUSTRALIA

MARGARET DAVIES, GRAEME F. WATSON, KEITH R. McDONALD,
MICHAEL P. TRENNERY AND GARRY WERREN

Davies, M., Watson, G.F., McDonald, K.R., Trennery, M.P. & Werren, G. 1993 06 30: A new species of *Uperoleia* (Anura: Leptodactylidae: Myobatrachinae) from northeastern Australia. *Memoirs of the Queensland Museum* 33(1): 167-174. Brisbane. ISSN 0079-8835.

Uperoleia altissima sp.nov. is from elevated sites on the Atherton and Windsor Tablelands in northeastern Queensland. The species is dentate and the call is short and pulsatile, features that distinguish it from all congeners. □ Anura, Myobatrachinae, Leptodactylidae. *Uperoleia altissima*, new species, advertisement call, external morphology, osteology.

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Uperoleia is a genus of small, fossorial frogs with highly glandular skin and a conservative morphotype. The nominate species, *U. marmorata*, was described by Gray (1841) and prior to 1981 was thought to have a wide ranging distribution throughout northern and eastern Australia. Tyler et al. (1981a,b) revised the genus and raised the number of recognised species from three to 18. They restricted the known distribution of *U. marmorata* to the type locality in northern Western Australia.

Davies et al. (1985) described a further species from the Pilbara whilst Tyler et al. (1986) suppressed *U. variegata* leaving 18 recognised species. These studies were confined to the Northern Territory and northwestern Western Australia and, thus, did not deal in any detail with eastern species (*U. rugosa*, *U. fimbrianus* and *U. laevigata*). These they restricted to their type specimens and localities, pending revision of the *Uperoleia* in eastern Australia. When this was completed (Davies & Littlejohn, 1986; Davies et al., 1986), *U. fimbrianus* was synonymised with *U. rugosa* and an additional six species were described. Presently, 23 species are recognised within *Uperoleia*.

During the study of eastern Australian *Uperoleia* a number of specimens were located in museum collections that could not be positively identified. Amongst these were five specimens in the Queensland Museum collection taken near Atherton, NE Queensland. These frogs appeared to be dentate, so resembling *U. fusca* in

Eungella National Park near Mackay, mideastern Queensland. However, they were too poorly preserved to permit positive identification.

In late January 1991, M.D., G.F.W. and K.R.McD. visited the Atherton Tableland and located a species of *Uperoleia* in the Millstream National Park. The species was dentate and conspecific with the indeterminate specimens encountered previously and with others collected at later dates from this site and the Windsor Tableland. Here we describe it as a new species

MATERIALS AND METHODS

Material cited here is deposited in the collections of the Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide (SAM), Museum of Natural History, University of Kansas (KU), and American Museum of Natural History, New York (AMNH). Measurements of specimens follow Tyler et al. (1981a). Measurements taken (in mm) were: eye diameter (E); eye to naris distance (E-N); internarial span (IN); snout to vent length (S-V); tibia length (TL).

Osteological data were obtained from cleared and stained material after the methods of Davis & Gore (1947) and Dingerkus & Uhler (1977).

The tape recording was made using a Sony TC-D5PRO cassette recorder (tape speed 4.76 cm/s) and Beyer M-88 cardioid dynamic microphone. Air wet bulb temperature (the effective temperature of a frog calling on land) was measured at the calling site using an electronic thermistor thermometer (Takara Digimulti Model

D611). The recording was analysed on a DSP 5500 digital Sona-Graph (Kay Elemetrics Corp.) using the in-built setup #10, with playback on a Nakamichi Dragon cassette recorder. Overall variations in tape speed (i.e. from recording to playback) are estimated at less than 0.5%; and the frequency responses of all audio-electronic components are close to linear within the relevant frequency range determined (based on the manufacturer's specifications). For each call, three primary attributes were determined: (i) duration as the interval from the beginning of the first pulse to the end of the last pulse (ms); (ii) number of pulses per note (direct count); and (iii) dominant frequency (Hz) as the maximum value of the spectrum of power between the cursors for the whole note. One derived attribute was determined — pulse rate [pulses/s determined from $(n-1 \text{ pulses})/\text{duration (in seconds)}$ measured from the beginning of the first pulse to the beginning of the last pulse]. Levels of resolution were less than 1ms for temporal aspects, and less than 40Hz for dominant frequency.

SYSTEMATICS

Family LEPTODACTYLIDAE Subfamily MYOBATRACHINAE *Uperoleia* Gray

Uperoleia altissima sp.nov. (Figs 1-7)

MATERIAL EXAMINED

HOLOTYPE: QM J55301, an adult male collected by M. Davies, K.R. McDonald & G.F. Watson in Millstream National Park (145°22'30", 17°38'30"), altitude 820m, Atherton Tableland, NE Queensland adjacent to the park entrance, 5.2km W of Ravenshoe, on 27 January 1991.

PARATYPES: QM J19851-52, Atherton (17°16', 145°29'), I.R. Straughan; QM J19855-57, Carbeen, Atherton Mareeba Rd (17°09', 145°26'), I.R. Straughan; QM J19858, 2km S of Mareeba (17°02', 145°02'), I.R. Straughan; QM J51780-4 (formerly QNPWS N15767-15771) Windsor Tableland (16°13'30", 144°58'30"), altitude 1160-1200m, K.R. McDonald, 16 January 1989; SAM R40144-46, KU 220086 same data as holotype; SAM R40147 (formerly QNPWS N58829) Blunder Ck, Wooroora, Atherton Tableland (145°26', 17°44'), J.W. Winter, 16 June 1987; AMNH 135814 (formerly QNPWS N58823) same data, 17 June 1987; SAM R34321 Western Distributor, Windsor Tableland (145°02', 16°15'), M.P. Trenerry & G. Werren, 11 January 1989; SAM R34318



FIG 1. A. Lateral and B. dorsal views of *Uperoleia altissima* sp.nov. (Holotype).

Millstream, Atherton Tableland, M.P. Trenerry & G. Werren, 15 January 1989; SAM R 34319 nr Ravenshoe, Atherton Tableland, M. Trenerry & G. Werren, 15 January 1989.

REFERRED MATERIAL: QM J31550-31553, nr Atherton, C. Corben.

DEFINITION

A small species (♂♂ 19-25mm S-V) characterised by the presence of maxillary teeth; moderately developed parotoid glands; darkly pigmented ventral surface excluding the pelvic patch ventromedially on thighs; grey dorsum with strong patterning; poorly to moderately exposed frontoparietal fontanelle; no webbing between the toes; vomerine fragments present; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent; advertisement call a single pulsed note of 2-3 pulses and a pulse repetition rate of 75.5 pulses/s.

DESCRIPTION OF HOLOTYPE

Maxillary teeth present. Vomerine teeth absent. Snout moderately short, slightly rounded when viewed from above, rounded in profile (Figs 1,2). Eye to naris distance greater than intermarial span (E-N/IN 1.29). Canthus rostralis moderately inconspicuous and straight. Nostrils dorsolateral,



FIG. 2. *Uperoleia altissima* sp.nov. in life (Holotype).

not surrounded by prominent lip. Tympanum not visible externally.

Fingers moderately long, slender, unwebbed, slightly fringed with prominent subarticular tubercles. In order of length $3 > 2 > 4 > 1$ (Fig. 3). Outer palmar tubercle large and prominent, inner indistinct. Hind limbs moderately short (TL/S-V 0.39). Toes long, unfringed and unwebbed. In order of length $4 > 3 > 5 > 2 > 1$ (Fig. 3). Metatarsal tubercles prominent; inner elongate, lying along axis of toe 1; outer rounded, acutely angled to long axis of foot. Subarticular tubercles prominent, not conical. Parotoid glands moderately developed; inguinal glands well developed; coccygeal glands not prominent; submandibular gland prominent and discrete (Fig. 1). Cloacal flap fimbriated and prominent.

Ventral surface coarsely granular. Male with unilobular submandibular vocal sac. Cream glandular nuptial pad on thumb.

Dorsum grey in preservative with apricot tipped tubercles and overlying black patterning. Black V-shaped marking between eyes and black suprascapular plicae. Limbs banded dorsally with black. Inguinal and femoral patches cream.

Ventral surface pigmented with small cream circular patches. Femoral region unpigmented (pelvic patch). Throat darkly pigmented with tiny white stipples.

In life, dorsum grey with black patterns. Dermal glands cream; eye golden. Inguinal and femoral patches flame scarlet (Smithe, 1975).

Dimensions: S-V 21.7; TL 8.4; E-N 1.8; IN 1.4; E 2.7.

VARIATION

Uperoleia altissima is a small species ranging 18.3-25.2mm S-V. The hind limbs are short (TL/S-V, mean = 0.38 (0.35-0.43) and eye to naris distance is always greater than internarial span (E-N/IN, mean = 1.40 (1.1-1.82)).

SAM R40144 (recorded specimen) differs from the other topotypic paratypes in that ventral pigmentation is not as dense and the dorsal pattern is not as discrete. In addition, this paratype has an abnormal third finger on the right hand, and the dorsum is more tubercular. SAM R34318, also from the type locality, also has sparse ventral pigmentation. The paratypes from near Atherton (QM J19858, J19855-56) have reacted to preserv-

TABLE 1. Characteristics of the advertisement call of an individual of *Uperoleia altissima* sp.nov. (SAM R40144) recorded on 27 January 1991, 5.2km W of Ravenshoe, NEQ. Means (with ranges of variation in parenthesis) of 20 successive calls are shown, Effective temperature at the calling site (air wet bulb) was 24°C.

No. of pulses	Duration (ms)	Pulse repetition rate (pulses/sec)	Dominant Frequency (Hz)
2.4 (2-3)	27.51 (21.90-31.30)	75.5 (69-80)	2560 (2560)

ative and are a dense uniform chocolate brown colour, masking all dorsal and ventral pigmentation. SAM R40147 has a smaller unpigmented pelvic patch which is slightly more anterior than in the other paratypes.

Differences between topotypic and Windsor Tableland material are very slight. The tips of dorsal tubercles tend to be cream rather than apricot (probably reflecting length of time in preservative). The inner palmar tubercles of most paratypes are masked by the unpigmented glandular nuptial pad, which extends around the base of the thumb. Slight fringing of the toes and minimal basal webbing between toes 2 and 3 and 3 and 4 is present in some material. Two of the Windsor Tableland paratypes, AMNH 135814 and the largest QM J19858 show greater development of the parotoid glands.

MATING CALL STRUCTURE

Twenty successive calls of the recorded individual were analysed and a summary of the call characteristics is listed in Table 1. The advertisement call of *U. altissima* is a short (mean duration 25.71ms), pulsatile call (mean pulse repetition rate 75.5 pulses/s) (Fig.4).

To the ear, the call is a sharp, loud click, repeated at a rate of about 90 calls/min. Among other species of *Uperoleia* whose calls have been described, seven (*U. aspera*, *U. glandulosa*, *U. littlejohni*, *U. lithomoda*, *U. mimula*, *U. minima* and *U. rugosa*) produce 'click' calls (short calls of Tyler et al., 1981a) with the call of *U. mimula* (reported ranges of variation are: duration 40-90ms; dominant frequency 2600-3300Hz; no. of pulses 3-5; pulse repetition rate 56-100 pulses/s; Davies et al., 1986) being most similar to that of *U. altissima*. The calls of these two north Queensland species are very similar except in call duration where there is no overlap in ranges of variation. Based on the calls analysed by Davies et al. (1986), the call of *U. mimula* is longer than the longer three-pulsed call of *U. altissima* (range 29.7-31.3ms). It should be noted that Davies et al. (1986) calculated pulse repetition rates using the formula $1000(\text{number of pulses})/\text{duration in ms}$. More accurate estimates of this derived attribute

are obtained from using the formula $1000(n-1)$ pulses/duration in ms, or, as has been used here: $1000(n-1)$ pulses/duration from the beginning of the first to the beginning of the last pulses in ms. The formula used here provides the best estimate, especially in situations where the pulse duration is large compared to the interpulse interval. For comparison, recalculation of pulse repetition rate of *U. altissima*, using the formula of Davies et al. (1986), gives values of 92.8 (87-101) pulses/s.

OSTEOLOGY (based on SAM R40146)

Skull well ossified. Medial ossification of dorsal sphenethmoid incomplete, overlain anteriorly by posteromedial edges of nasals; ventrally extends about 1/3 length of orbit posteriorly. Prootic not fused with exoccipital; epiotic eminences prominent. Exoccipital not fused dorso- or ventromedially. Crista parotica short, stocky; confluent laterally with long unexpanded otic ramus of squamosal. Shallow groove of carotid canal posterolaterally on frontoparietals (Fig. 5). Frontoparietal fontanelle exposed anteriorly as inverted roughly triangular area, roofed medially

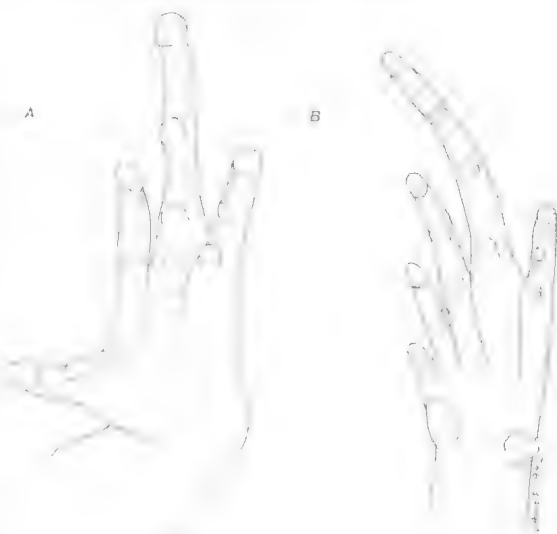


FIG. 3. A. Palmar view of hand. B. Plantar view of foot of *Uperoleia altissima* sp.nov. (Holotype).

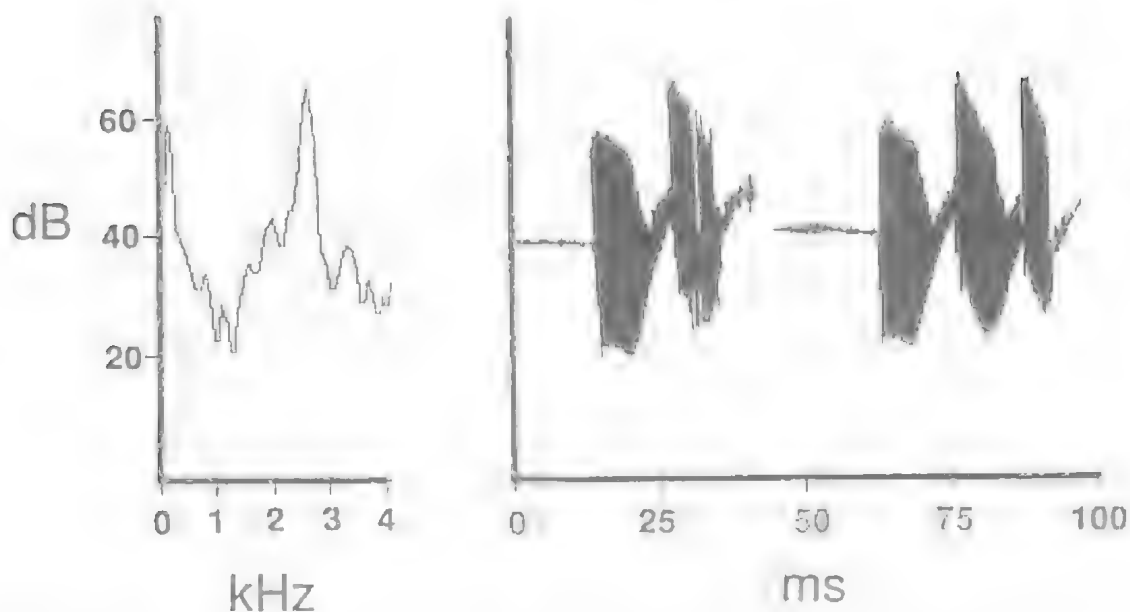


FIG. 4. Power spectrum and wave form of two advertisement calls of *Uperoleia altissima* sp. nov. (SAM R40144), recorded on 27 January 1991, 5.2 km W of Ravenshoe, NEQ, at a wet bulb air temperature of 24°C. Note that the ordinate for the wave form display is not labelled because it depicts a relative linear scale in volts.

and exposed again as an approximately diamond-shaped area posteriorly. Anterior extremities of frontoparietal fontanelle about level of anterior extremities of pterygoid. Posterior extremity undefined. Frontoparietal elements well ossified reaching posterior extremities of nasals anteriorly.

Nasals well ossified, approximately triangular, closely applied medially, overlying sphenethmoid posteriorly. Maxillary process poorly developed not reaching pars facialis of maxilla. Palatines moderately broad; reduced laterally, not in contact with pars facialis of maxilla but overly sphenethmoid medially.

Parasphenoid robust. Cultriform process moderately broad, truncated terminally, not reaching level of medial extremities of palatines. Alae robust, deep, slightly angled posterolaterally reaching level of extremities of medial rami of pterygoids (Fig. 5).

Pterygoid moderately robust; slender anterior ramus in long contact with well-developed pterygoid process of maxilla. Medial ramus moderately broad, acuminate. Posterior ramus moderately broad. Small cartilaginous quadrate at articulation of base of squamosal and quadratojugal. Squamosal shaft robust; short knobbed zygomatic ramus; long unexpanded otic ramus.

Maxilla and premaxilla dentate. Teeth sparse toward pterygoid process of palatal shelf of maxilla. Teeth relatively small. Alary process of premaxilla moderately slender, not inclined posteriorly. Vomerine processes of palatal shelf of premaxilla well developed, articulating medially. Pars facialis of maxilla moderately deep posteriorly, shallower anteriorly; lacking preorbital process.

Remnant fragments of dentigerous processes of vomers medial to palatines. Bony columella extremely robust (Fig. 5).

Pectoral girdle arciferous and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Left clavicle previously fractured, right slender, curved; both closely applied medially. Coracoids robust, widely separated medially. Scapula bicapitate, curved, approximately same length as clavicle. Suprascapula about one half ossified.

Eight procoelous non-imbricate presacral vertebrae. Sacral diapophyses poorly to moderately expanded. Relative widths of transverse processes: III > IV > II = V = VI > VII > VIII.

Urostyle crest about 2/3 length of urostyle. Ilium with no dorsal crest. Dorsal prominence broadly obtuse; dorsal protuberance poorly-developed dorsolaterally (Fig. 6A).



FIG. 5. A. Dorsal and B. ventral views of the skull of *Uperoleia altissima* sp. nov. (SAM R40146).

Humerus with well-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3; distal tips of terminal phalanges knobbed. Carpus of six elements, moderate torsion (Fig. 7). O. ulnare and O. radiale present. O. radiale larger of two. Both articulate with O. radioulna proximally and with each other distally. Distally both articulate with large transversely elongate O. centrale postaxiale. O. radiale articulates laterally with O. centrale preaxiale. O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V; moderately well-developed lateral flange extends from lateroproximal corner. Palmar sesamoid anteroventrally. O. centrale preaxiale articulates laterally with O. centrale postaxiale and with unfused carpal elements of O. distale carpale 2 and 3 and laterally with basal prepollical element.

Phalangeal formula of foot 2,2,3,4,3. O. tibiale and fibulare elongated elements fused at either end. O. tibiale extends as far as distal end of O. fibulare. Three distal tarsal elements present. Lateral elements largest, lying at base of O. metatarsus III, extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lies between bases of O. metatarsi II and I. Medial element lies at the base of O. metatarsus I, articulating also with O. centrale prehallucis. Distal prepollical element subulate extending for about 2/3 length of O. metatarsus I (Fig. 7). Two sesamoids at base of prehallux.

Hyoid plate about as broad as long. Alary processes broad, not pedunculate. Anteromedial processes of anterior hyale slender and moderately long. Posterolateral processes of plate elongate. Posterior cornua long and ossified (Fig. 6B).

VARIATION IN OSTEOLOGY

Three paratypes were examined for osteological variation: QM J19581, 19587 and 51782. All are dentate but there are fewer teeth than in the described specimen. Maximum development is on the premaxilla and development decreases posteriorly. The posterior exposure of the frontoparietal fontanelle is minimal in J51782, but is the same as in the described paratype in the other two. Ossification of the nasals and of the sphenethmoid is slightly less in J51782 than that described. Development of the zygomatic ramus of the squamosal is slightly less in J19852 whilst the pars facialis of the maxilla is less crenate in J19851. Vomerine fragments are difficult to detect in this same paratype.

ETYMOLOGY

The specific name is derived from the Latin *altus* meaning high, in reference to the elevations at which the species has been collected.

COMPARISON WITH OTHER SPECIES

Uperoleia altissima is a dentate species, a feature shared by *U. marmorata*, *U. mjobergi*, *U. micromeles*, *U. tyleri*, *U. martini*, *U. laevigata* and *U. fusca*.

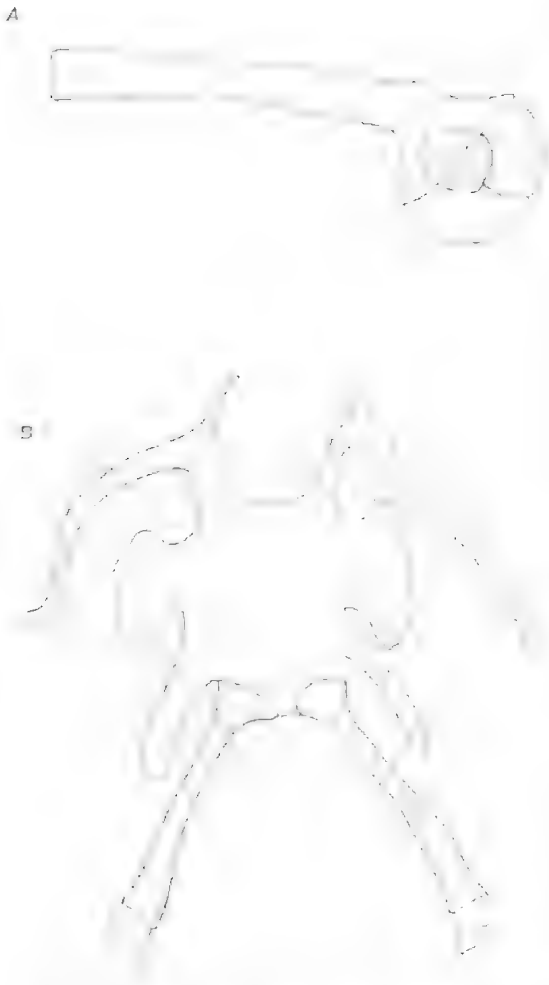


FIG. 6. A. Lateral view of the ilium (SAM R40146). B. Ventral view of the hyoid (QM J51782) of *Uperoleia altissima* sp. nov.

U. marmorata and *U. mjobergi* are confined to the Kimberley Division of Western Australia. Dentition in *U. micromeles* is sparse, similar to that found in *U. altissima*. This species is confined to desert areas in central Australia. It has very broadly spaced nasals ($E-N/IN < 1$) and broad more elongate palatines. In addition, the shape of the nasals is unusual within *Uperoleia*. *U. tyleri* and *U. martini* are large species with hypertrophied parotoid glands and uniform ventral pigmentation. *U. altissima* is most similar morphologically to *U. laevigata* and *U. fusca*. Both these species have long calls of 32-68 or 20 pulses. In addition, both have a completely-roofed frontoparietal fontanelle and a well-devel-

oped preorbital process on the pars facialis of the maxilla.

U. altissima is most similar in call structure to *U. mimula*. This is an edentate species in which vomerine fragments are absent and which has an extremely well-developed dorsal prominence on the ilium, features not shared by *U. altissima*.

HABITAT

The type locality is medium eucalypt woodland with *Themeda triandra* and *Imperata cylindrica* (Type 16O of Tracey, 1982) and is located on Glen Gordon Volcanics. Windsor Tableland vegetation is low to medium eucalypt woodland (Type T6S) on Mareeba granites. This area was highly disturbed being near a creek system with numerous mining tracks

DISTRIBUTION

U. altissima has been located only at elevated sites on the Atherton and Windsor Tablelands, NE Queensland.

DISCUSSION

Uperoleia comprises a number of cryptic species pairs including *U. rugosa* and *U. capitulata*, *U. tyleri* and *U. martini*, *U. laevigata* and *U. fusca*, *U. inundata* and *U. arenicola*, *U. mimula* and *U. lithomoda*. The recognition of *U. altissima* adds a third example to this latter cryptic species pair.



FIG. 7. A. Dorsal view of bones of hand. B. Dorsal view of bones of foot of *Uperoleia altissima* sp. nov. (SAM R40146).

Morphologically *U. mimula* and *U. lithomoda* are extremely similar (Davies et al., 1986) and close similarity in call structure between *U. mimula* and *U. altissima* exists. The presence of dentition in *U. altissima* may be the only feature that will aid field identification. Both *U. mimula* and *U. altissima* have been collected on the Windsor Tableland. The occurrence in sympatry of species with such similar call structures occurs also with *U. tyleri* and *U. martini* in southeastern Australia. To the ear on hot nights, calls of *U. mimula* and *U. lithomoda* are difficult to distinguish adding to the difficulty of field identification of this cryptic group of species.

The nature of the dentition in *U. altissima* has been shown to be a paedomorphic condition (Davies, 1989) together with a number of osteological features common to dentate species. These include the presence of vomerine fragments and the knobbed nature of the zygomatic ramus of the squamosal. Such features influenced by heterochrony provide explanations for the morphological divergences found within this enigmatic group of frogs.

ACKNOWLEDGEMENTS

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THE SPINNING FIELD AND STRIDULATING APPARATUS
OF PENULTIMATE MALE *MACROGRADUNGULA MOONYA*
(ARANEAE: AUSTRORHINOIDEA: GRADUNGULIDAE)

VALERIE TODD DAVIES

Davies, V.T. 1993 06 30: The spinning field and stridulating apparatus of penultimate male *Macrogradungula moonya* (Araneae: Austrochiloidea: Gradungulidae). *Memoirs of the Queensland Museum* 33(1): 175-178. Brisbane. ISSN 079-8835.

The cribellum of penultimate ♂ *Macrogradungula moonya* is essentially bipartite but has an undivided spinning field. On the ALS there is a median cluster of about 20 major ampullate gland spigots, 2 of which are larger than the rest; on the PMS there is a single large minor ampullate spigot and 2 patches of paracribellar spigots (about 60). There is a stridulating file or ridges on the distal outface of the chelicera and a row of 'plucking' setae arising from tubercles on the prolateral surface of the palpal femur. □ *Araneae, Austrochiloidea, Gradungulidae, spinning field, stridulating apparatus.*

Valerie Todd Davies, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 26 November, 1992.

Platnick et al. (1991) included some SEMs of the spinnerets of a juvenile *Macrogradungula moonya* in their study of haplogyne spinnerets. Apart from the possession of a cribellum and paracribellar spigots, this was shown to have greater differentiation of spigots than the ecribellate gradungulids. The penultimate ♂ (more than 20mm in body length) was expected to show this more clearly.

SPINNING FIELD

The cribellum (Figs 1,2) is narrow, six times as wide as long; the cribellar spigots are very small, close together and strobilate (Figs 3,4). The anterior spinnerets (ALS) (Figs 5,6) have a median field of about 20 major ampullate gland spigots (Map) of which 2 anterior spigots are a little larger than the rest; the ampullate spigot field is separated by a ridge from numerous piriform spigots (pi). The median spinnerets (PMS) (Figs 7,8,10) have one large minor ampullate spigot (map) with 5 aciniform spigots near its base and 11 aciniform spigots (ac) posterior to it; a large cluster of about 40 paracribellar spigots (pc) antero-medially and a further cluster of about 20 paracribellar spigots latero-distally. The posterior spinnerets (PLS) (Figs 9,11,12) have many aciniform spigots; 2 proximal spigots have wider bases than the others; tartipores (t) which are thought to be traces of spigots present in previous instars (Yu & Codrington, 1990) are present.

Compared with the juvenile ♀ (Platnick et al., 1991), a great increase in the number of spigots on all spinnerets is found. The bases of the parac-

ribellar spigots are long and cylindrical, suggesting that the flat sail-like bases in the smaller spider may have been mechanically compressed to that shape.

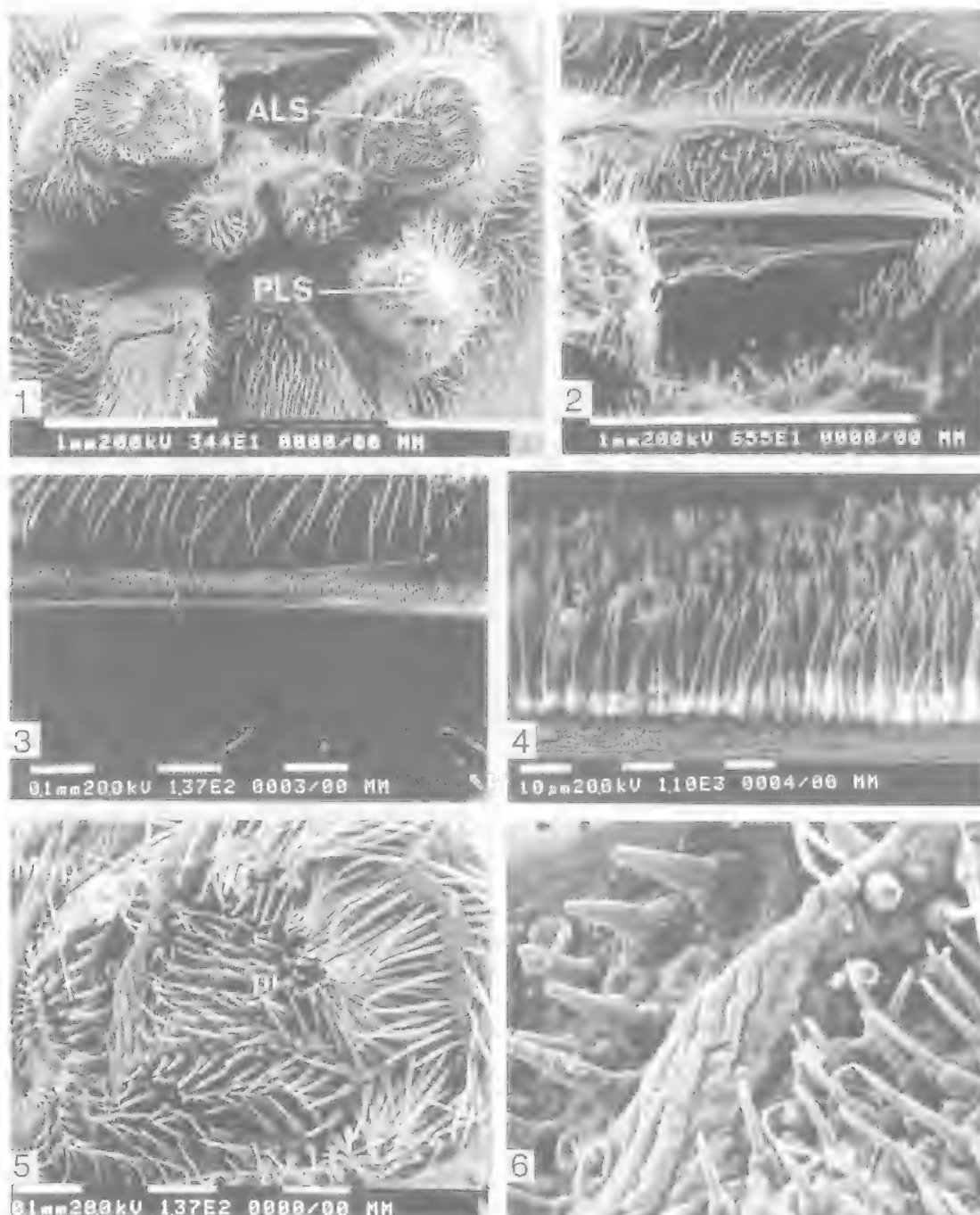
Examination of the ♀ holotype under a light microscope revealed a similar pattern to the penultimate ♂ with an even greater number of piriform spigots on the ALS. The PMS have one large minor ampullate spigot with 2 patches of spigots (paracribellar) and a large number of aciniform spigots becoming larger proximally. The PLS have many aciniform spigots also increasing in size proximally.

The presence of about 20 major ampullate gland spigots on the ALS is similar to that found in the hypochiloids; *Hickmania* and the South American austrochiloids have only 2 Map. Spigots on the PMS are like those in austrochiloids and have the same sculpturing pattern on the base; neither a minor ampullate spigot nor paracribellar spigots are found in the hypochiloids (Platnick et al., 1991). In the ecribellate gradungulids the minor ampullate spigot is lost along with the cribellum and paracribellar spigots.

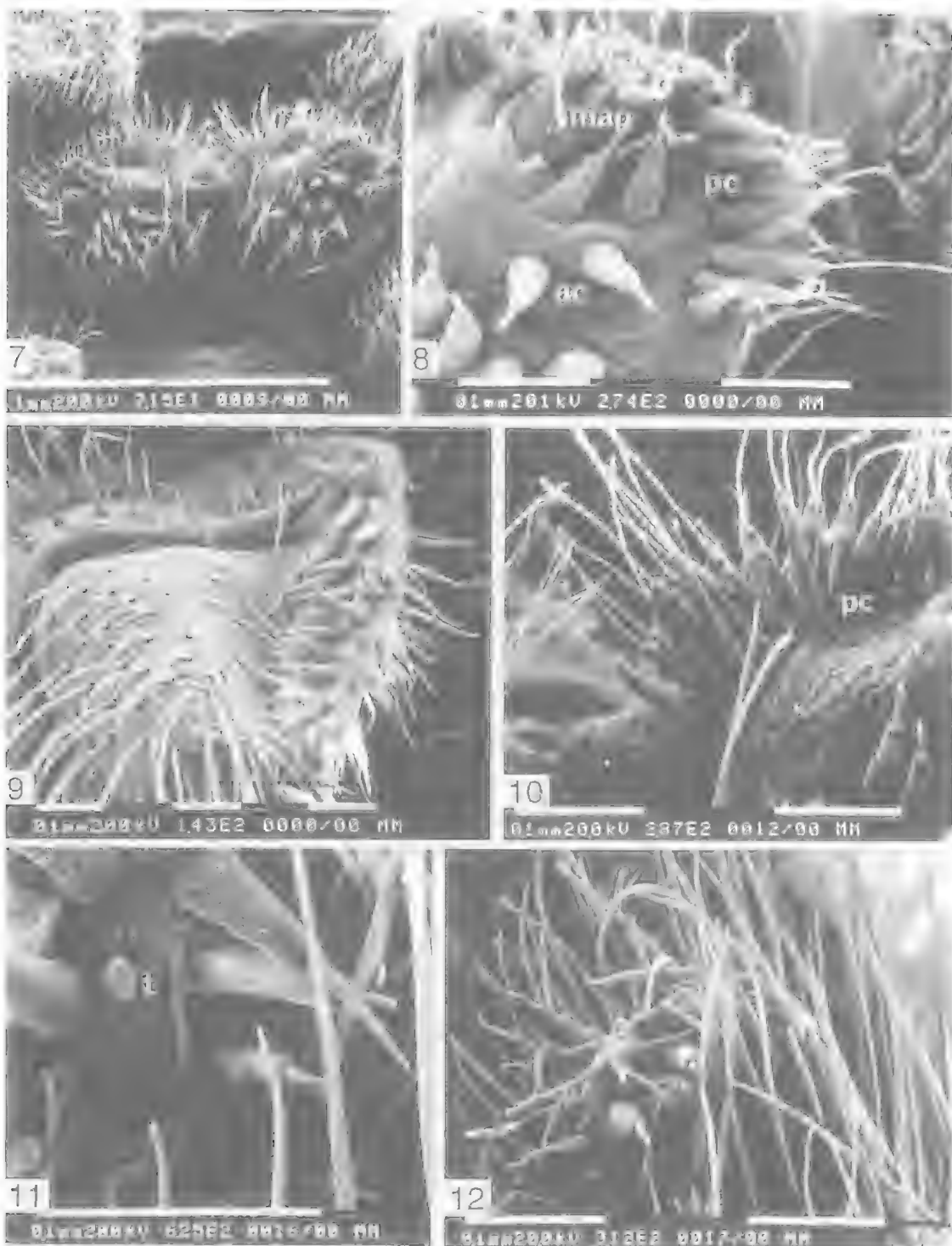
The cribellum is homologous with the anterior median spinnerets of liphistiids and likewise the colulus when present is also homologous (Lehtinen, 1967: 398). Glatz (1972) showed that the paired muscles supplying the cribellum still persist in the colulus i.e. its bipartite history is evident. The cribellum is more than a plate of spigots; it is a movable plate supplied by muscles to each side (Glatz, loc. cit.). In the cribellum even though the cribellar field of spigots may be entire (hypochiloids and austrochiloids) the whole

structure is essentially bipartite. This is clearly illustrated in *Macrogradungula moonya*, where the median posterior edge of the cribellum is

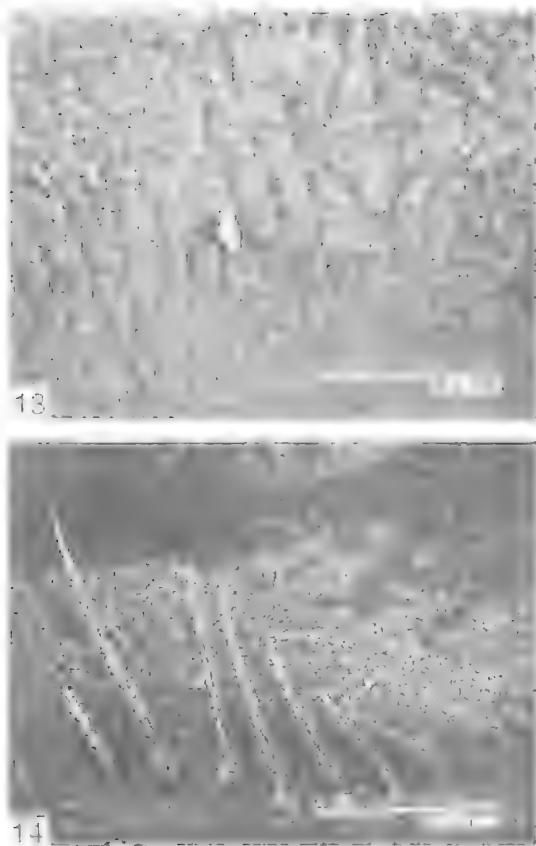
clearly notched (Fig. 2) and the cribellar field is narrow and entire but constricted centrally (Fig. 3) suggesting that separate fields have joined.



FIGS 1-6, penultimate ♂ *Macrogradungula moonya*. 1, spinning field. 2, cribellum. 3,4, cribellar spigots. 5,6, ALS, major ampullate and piriform spigots.



FIGS 7-12, penultimate ♂ *Macrogradungula moonya*. 7,8,10, PMS. 9,11,12, PLS.



FIGS 13,14, penultimate ♂ *Macrogradungula moonyi* stridulatory apparatus. 13, ridged area of chelicera. 14, 'picks' on palpal femur.

Transverse serial sections of the abdomen show paired muscles from a posterior sclerite to the cribellum. Further if we consider the cribellum to be the homologue of the anterior median spinnerets and the colulus to be a functionless remnant of the cribellum then it suggests that the bipartite spinning field may be the pleisiomorphic state and the single field derived. In recent cladistic hypotheses, Platnick et al. (1991) and Coddington & Levi (1991) regard the single field as pleisiomorphic because the cribellar field of hypochoiloids is entire. This single field is also found in the deinopoids, some dictynoids and some claw-

tufted spiders; it may have arisen more than once and is unlikely to be reversible.

STRIDULATING APPARATUS

Contrary to Gray (in Forster, Platnick & Gray, 1987: 90), a stridulatory file consisting of parallel ridges is present on a small area on the distal outface of the chelicera, near the dorsal surface (Fig. 13). Picks in the form of enlarged setae on tubercles are found on the prolateral surface of the palpal femur (Fig. 14).

ACKNOWLEDGEMENTS

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FIRST SKULL OF A SPECIES OF *HIPPOSIDEROS* (*BRACHIPPOSIDEROS*)
(MICROCHIROPTERA: HIPPOSIDERIDAE), FROM AUSTRALIAN MIOCENE
SEDIMENTS

SUZANNE J. HAND

Hand, S.J. 1993 06 30: First skull of a species of *Hipposideros* (*Brachipposideros*) (Microchiroptera: Hipposideridae), from Australian Miocene sediments. *Memoirs of the Queensland Museum* 33(1): 179-192. Brisbane. ISSN 0079-8835.

Cranial material of a species of *Hipposideros* (*Brachipposideros*) is figured and described for the first time. The skull of the Australian Tertiary leaf-nosed bat *Brachipposideros nooraleebus* Sigé, Hand & Archer, 1982 is described on the basis of new material recovered from the type locality on Riversleigh Station, northwestern Queensland. As part of this study, morphological differences between three hipposiderids, *Hipposideros* (*Brachipposideros*) *nooraleebus*, *Rhinonictis aurantius* and *Hipposideros* (*Hipposideros*) *speoris*, are reported. *Hipposideros* (*B.*) *nooraleebus* appears to be more similar to *R. aurantius* than to its congener *H. speoris*. □ Tertiary, fossil, bat, skull, Hipposideridae, Riversleigh, Microsite.

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In 1982, the Tertiary leaf-nosed bat *Hipposideros* (*Brachipposideros*) *nooraleebus* was described from collections made between 1976 and 1981 from the Microsite locality on Riversleigh Station, northwestern Queensland (Sigé, Hand & Archer, 1982). The Microsite deposit, which contains the Nooraleeba Local Fauna (Sigé et al., 1982), is one of more than 150 Oligo-Miocene fossil-bearing, freshwater limestone deposits on Riversleigh Station (Archer et al., 1989, 1991).

Hipposideros (*Brachipposideros*) *nooraleebus* was the first Australian Tertiary bat to be named and the first species of the subgenus *H.* (*Brachipposideros*) recorded from outside of France. In France, the subgenus is known from six other species also of Oligo-Miocene age (Sigé, 1968; Legendre, 1982; Sigé et al., 1982). The Australian bat was found to most closely resemble the French Burdigalian (early middle Miocene) species *H. (B.) aguilari* (Sigé et al., 1982). The appearance of closely related taxa in Australian and European sediments is enabling intercontinental biocorrelation of Australian Tertiary mammal-bearing deposits. Sigé et al. (1982) regarded *Brachipposideros nooraleebus* to be a possible ancestor of northern Australia's living endemic Orange Horseshoe Bat *Rhinonictis aurantius*.

In 1982, *B. nooraleebus* was described, like the French *Brachipposideros* species, mainly on the basis of its teeth. By 1982, thousands of well-preserved dentaries and partial maxillae had been collected from Microsite. Subsequently, the deposit yielded partial skulls referable to this spe-

cies. In this paper, cranial material of *H. (Brachipposideros)* is described for the first time and compared with the skulls of *R. aurantius* and the type species *Hipposideros speoris speoris* of India and Sri Lanka.

Dental nomenclature follows Sigé et al. (1982). Skull terminology is modified from Sigé (1966), Barghoorn (1977) and Novacek (1986, 1991). The prefix QMF refers to the fossil collections of the Queensland Museum, Brisbane. Repositories of comparative Recent specimens are indicated by prefixes as follows: M, Australian Museum, Sydney; CM, CSIRO Division of Wildlife and Ecology, Canberra; AR, temporarily held in collections at the University of New South Wales. Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1989, 1991).

SYSTEMATICS

Hipposideros* (*Brachipposideros*) *nooraleebus
Sigé, Hand & Archer, 1982
(Figs 1-4, Table 1)

REFERRED SPECIMENS

QMF19034, a rostrum preserving the palate, left M¹-M³ and alveoli for P¹ and anterior roots for left zygomatic arch (Figs 1A, 2A, 3); QMF19035, a braincase preserving the skull roof and basicranium with petrotic bones in situ (Figs 1B, 2B, 3); QMF19036, a right maxillary fragment with C¹-M³; QMF19037, a left maxillary fragment with P¹, M¹, M³ and anterior zygomatic arch; QMF19038, a rostrum (edentulous) with

anterior zygomatic arch; QMF19039, a rostrum with right P^4-M^3 and left M^1-M^2 ; QMF19040, a left maxillary fragment with C^1-P^4 and M^2-M^3 ; QMF19041, a rostrum with left M^3 and anterior zygomatic arch; QMF19042, skull fragment with left P^4-M^3 and anterior dorsal cranium; QMF19043, dorsal cranium; QMF19044, ankylosed left and right premaxillae (Fig. 4); QMF19045, a right premaxilla; QMF19046, an upper I^1 ; QMF19047, a lower I^1 ; QMF19048, a lower I^2 ; QMF19049, posterior skull fragment preserving basicranium, glenoid surface, post-glenoid process and posterior roots of zygomatic arch; QMF19050, a left petiotic; QMF19051, a right petiotic.

LOCALITY, STRATIGRAPHIC POSITION AND AGE

Microsite occurs approximately 15m south of the southern end of the exposure of Carl Creek Limestone at Tedford's (1966) Site D within the Tertiary sequence of freshwater limestone sediments on Riversleigh Station, northwestern Queensland. Sigé et al. (1982) interpreted the age of the Microsite sediments, and the contained Nooralceba Local Fauna, to be of middle Miocene age, largely on the basis of the interpreted stage of evolution of fossil marsupials preserved with the Microsite bats. The Microsite limestone was interpreted to represent a distinct facies with an uncertain stratigraphic relationship to the Carl Creek Limestone of the nearby Site D (also interpreted then to be of middle Miocene age; Archer, 1981).

Ongoing stratigraphic and biocorrelative work on the Riversleigh Tertiary limestone sequences, including study of rich mammal-bearing deposits

discovered since 1983 (Archer et al., 1989, 1991) led to a reinterpretation of the age and nature of the Microsite deposit as an early Miocene cave deposit intruded into slightly older System A sediments which themselves probably date from the late Oligocene to early Miocene (Archer et al., 1989, 1991).

ASSOCIATED FAUNA AND TAPHONOMY

Hipposideros (Brachyhipposideros) nooralcebus is represented in the Microsite deposit by tens of hundreds of individuals. It appears to be the only hipposiderid in the Nooralceba Local Fauna, which also contains the megadermatid bat *Macroderma godthelpi* (Hand, 1985) as well as small fish, crocodiles, turtles, passerine birds, dasyurids, potoroids, a perameloid and a petaurid (Rich et al., 1991). Postcranial and dental remains of *B. nooralcebus* are commonly very well preserved in the deposit, many being complete. However, uncrushed cranial material of *B. nooralcebus* is relatively rare. Microsite fossils are particularly fragile compared with those from Riversleigh's other Oligo-Miocene bat-bearing deposits. The fossils appear to be demineralised, possibly the result of post-depositional leaching or, alternatively, a unique palaeochemistry of the depositional environment.

DIAGNOSIS

See Sigé, Hand & Archer (1982: 152).

DESCRIPTION

The comments made here are intended to supplement the accompanying photographs and drawings. The skull is known from a number of

TABLE 1. Measurements of skull and upper dentition of *H. (Brachyhipposideros) nooralcebus*, Microsite, Riversleigh Station. L, length; w, width; d, distance. In mm.

QMF	19034	19035	19036	19037	19038	19039	19040	19041	19042
						right	left		
C^1-M^1L			5.79				5.52		
P^4-M^1L			4.34	1.40		4.36	4.30		4.56
M^1-M^1L	3.66		3.42	3.51		3.84			
P^4L			1.07	1.03		1.07	1.05		1.01
M^1L	1.34		1.40	1.46		1.35	1.47		1.45
M^2L	1.31		1.22			1.34	1.40	1.31	1.36
M^3L	1.02		0.98	1.02		0.92	0.93	1.00	1.01
Palatall.	1.63		1.77		1.47	1.69		1.77	
Interorbitalw	1.97		2.12					2.10	
Maxillary		7.95							
Petiotew		2.88							
Interpetiotew		1.43							

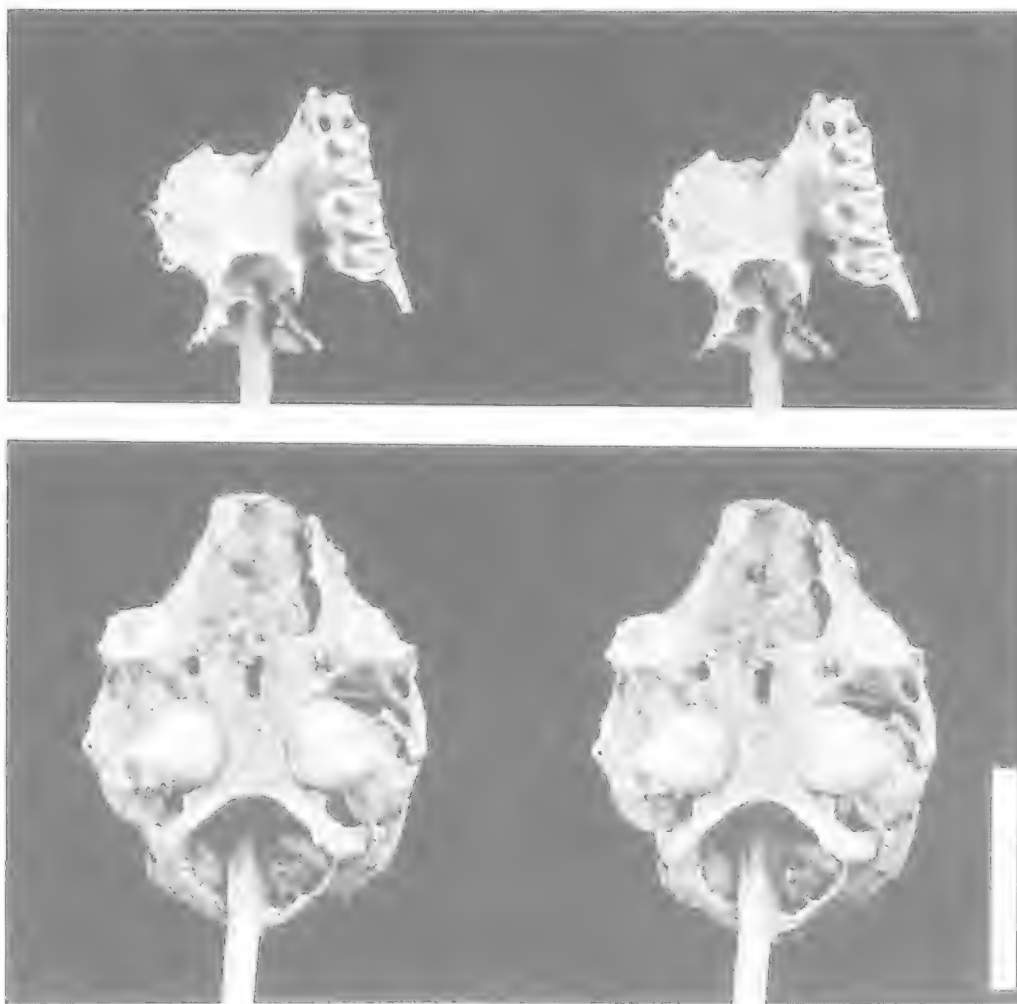


FIG. 1. *Hipposideros (Brachhipposideros) nooraleebus*, Microsite, Riversleigh Station, northwestern Queensland: A, QMF19034, ventral view, stereopair; B, QMF19035, ventral view, stereopair. Bar indicates 5mm.

incomplete specimens. The most complete of these are QMF19034, a rostrum preserving the nasals, palate, anterior root for the left zygomatic arch, left M^{1-3} and alveoli for P^4 , and QMF19035, a braincase preserving the skull roof, basicranial and ear regions, with periotics in place. Matrix obscures part of the right ear region but has been left in place for structural support. The description is based primarily on these two specimens but other referred specimens (see list above) provide additional information. There is no evidence of crushing of cranial material but some breakage has occurred. Some details of the medial skull region are lacking.

It has not been possible to determine the precise limits of each bone in the skull. In microchiro-

pteran bats, sutures between bones of the skull fuse completely early in development, and no juvenile specimens of *Brachhipposideros nooraleebus* have yet been recovered. However, as a guide for interpreting approximate bone boundaries in the fossil hipposiderid, several juvenile rhinolophoids were examined in this study, i.e. specimens of *Hipposideros diadema* (M20478), *Rhinolophus megaphyllus* (AR17575) and *Macroderma gigas* (M11762, M27675).

General outline and proportions. The skull is small, slender and strongly constricted in the interorbital region. The rostrum is relatively broad and long. The rostral length is approximately half the length of the braincase and its greatest width, at the level of the most anterior point of the orbit

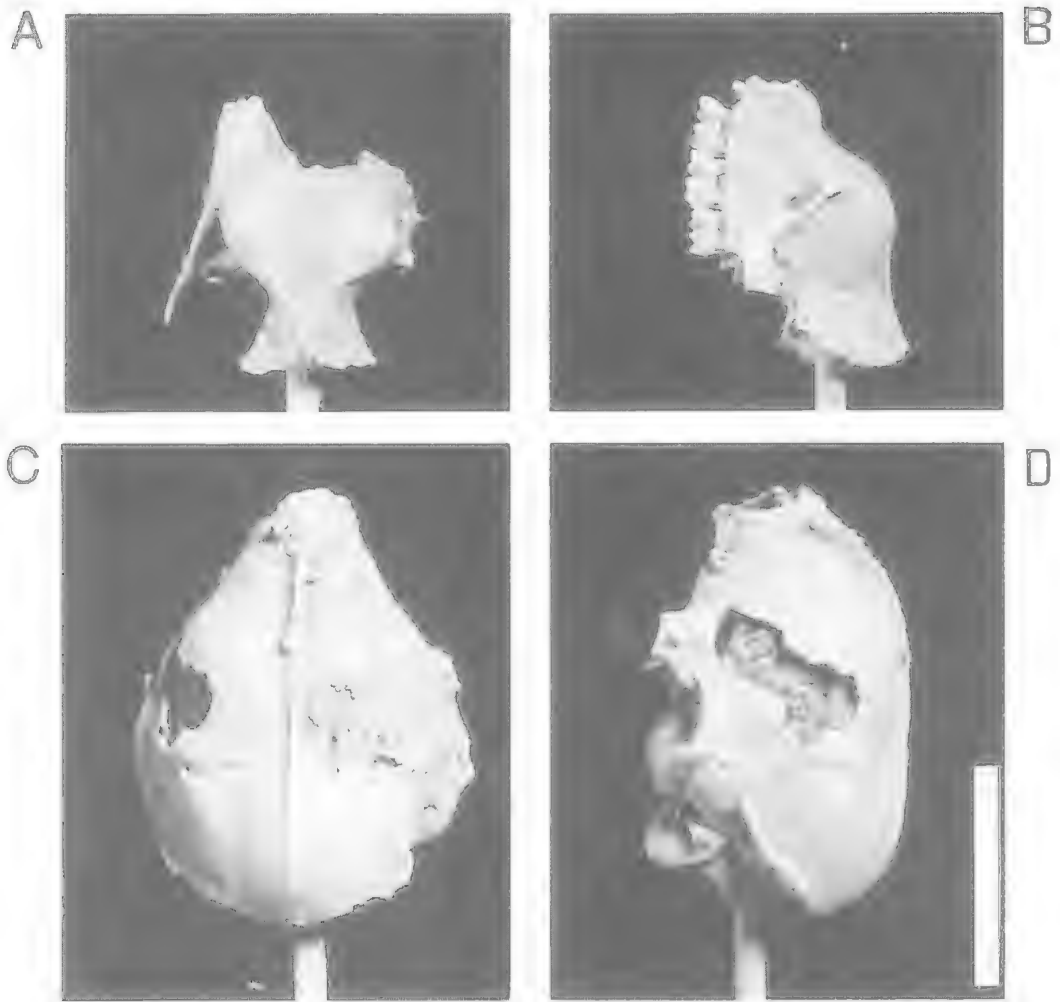


FIG. 2. *Hipposideros* (*Brachipposideros*) *nooraleebus*, Microsite, Riversleigh Station: A-B, QMF19034, dorsal and lateral views; C-D, QMF19035, dorsal and lateral views. Bar indicates 5mm.

(the lacrimal foramen), approximately two-thirds the mastoid width and more than twice the interorbital width. In height, the rostrum is lower than the braincase. The braincase is broadest across the mastoids (at the level of the post-tympanic processes). The maximum zygomatic width is not known.

Rostrum. The rostrum is square in outline, being approximately as long as wide and with subparallel lateral borders. It is deeply notched anteriorly, this indentation describing a broad arc between the maxillae. Conspicuous rostral inflations are separated by a broad, shallow trough delimited by well-developed supraorbital ridges. These are better defined posteriorly than anteriorly

where they are attenuated by the nasal inflations. In the trough, at a point approximately midway between the anterior margin of the nasals and the junction of the supraorbital ridges, is a small, unpaired foramen. The rostral inflations are most conspicuous in lateral view, such that in profile the face is not gently inclined but rises almost vertically from the level of the palate to the maximum height of the rostrum.

The zygomatic arch extends onto the face as a very thin arch that joins the lateral wall of the maxilla. Under this arch (i.e. enclosed by a narrow bar of bone) opens the anteroposteriorly elongated infraorbital foramen. Hidden in lateral view by the arch, two orifices open in the lateral

wall of the face at the front of the orbital fossa. The first, the lacrimal foramen, opens under the anterior attachment point of the arch at the edge of the circumorbital rim, and is separated from the infraorbital foramen by only a thin wall of bone. Posteriorly, at the ventral part of the anterior recess of the orbital fossa, is the second orifice: a broad, deep fossa that exposes the maxillary bone covering the roots of the posterior cheekteeth. Medial to this, at the most anteroventral point of the orbit, is a post-palatal foramen which leads through into the palate. More posterodorsal and medially, in the lateral wall of the interorbital constriction, two small foramina open into a long, curved, shallow groove that leads posterodorsally from the post-palatal foramen to the optic foramen. Dorsal and medial again in the interorbital region is a deeper, shorter, anteroposteriorly directed sinus into which a number of foramina also open at the level of, or just posterior to, the cribriform plate of the ethmoid. These foramina appear to vary in number, form and position (and from one side of the skull to the other) perhaps varying epigenetically.

Palate. The palate is short. The toothrows are not convergent anteriorly. At the palate's anterior edge is a deep, V-shaped indentation, which extends posteriorly to the level of the posterior face of M^1 , for the junction with the premaxillae. The palate's posterior border has two deep posterolateral indentations that extend anteriorly to at least the level of the anterior face of M^3 . Each closely skirts M^3 and forms a recess beside the palatine. The posterior extension of the midline of the palate is level with the anterior face of M^1 ; a medial palatal spine is variably developed. The maximum width of the palate is at the level of M^2 . The palate is almost flat though slightly concave longitudinally. The most constant and well developed palatal foramina are medial to the anterior face of M^1 . Other foramina appear to be variable but a fossa medial to M^{2-3} is usually perforated by a number of foramina and on the midline, medial to the posterior face of M^1 , an unpaired foramen occurs in some specimens.

Premaxillae. The ankylosed premaxillae comprise a small, loose element that bears a single pair of incisors. The best preserved specimens are QMF19044 (Fig. 4) and QMF19045 but the incisors have been lost from both. The premaxillae gently flare anteriorly. The incisor alveoli occur at the anterior edge in a medial position. Posteriorly, two thin premaxillary processes probably do not fully enclose large anterior palatal foramina. The premaxillae are very thick with, at their line

of contact, a distinct crest on the dorsal surface. The dorsal surface is convex in both horizontal and longitudinal axes. In anterior view, the convexity is rather gentle. In lateral view, it is more acute and is accentuated by the distinct posteriorly directed crest. This reaches its maximum height about one-third the distance from the premaxillae's anterior edge. The incisors would have been directed ventrally. The ventral surface of the premaxillae is generally gently concave longitudinally but posteriorly it is domed.

Nasals. The inflated nasal cavities are bilaterally symmetric, being divided by a median septum. The dorsal border of the septum parallels the palate rather than the contour of the face. Posteriorly, the septum fuses with the anteriorly inclined cribriform plate. The posterior face of the plate is deeply concave and perforated by many foramina of varying sizes. The endocranial space is arched over the inclined cribriform plate. Posteriorly, curved lateroventral extensions of the median septum (subethmoidal shelves) partially separate each nasal cavity into a ventromedial respiratory section and more extensive dorsal and lateral olfactory sections. The latter are further subdivided, by a thin ethmoidal lattice, into anterior and posterior chambers. The ethmoturbinal mass appears to have been very simple but is not well enough preserved to be confidently described. Above the cribriform plate, the nasal cavity expands into a broad chamber roofed by the frontals.

Interorbital and pterygoid region. Immediately to the rear of the face and between the orbital fossae, the braincase narrows. The point at which the two supraorbital crests unite (i.e. where the sagittal crest originates) is clearly posterior to the point of narrowest constriction. The pterygoid wing, sloping ventrally and laterally, forms the posteromedial wall of the orbital fossa. The side wall of the skull is pinched in between the cranium and the palatine and pterygoid wings, and hence the optic foramen and sphenorbital fissure open ventrally from the braincase. The sphenorbital fissure was evidently long and wide, a very narrow bony bridge separating it from the large, almost semicircular optic foramen. Immediately lateral to the most anterolateral margin of the sphenorbital fissure is a small, round foramen. Anterior to the optic foramen is the cribriform plate of the ethmoid. Small pterygoid processes occur at a point laterally in line with the junction of the supraorbital ridges and posterior to M^3 at a distance approximately equal to the length of M^3 . If hamular processes were present they are now

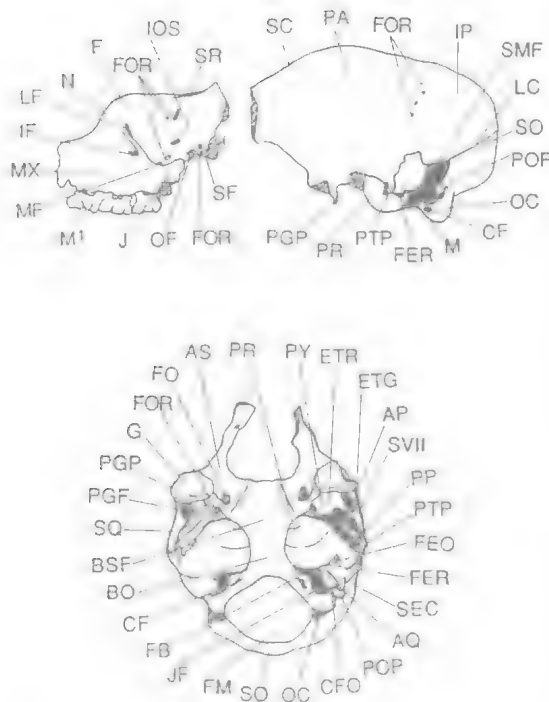


FIG. 3. *Hipposideros* (*Brachipposideros*) *nooraleebus*, Microsite, Riversleigh Station. Top, QMF19034 and QMF19035, lateral views. Bottom, QMF19035, ventral view. AP anterior process; AQ aqueductus cochleae; AS alisphenoid; BO basioccipital; BSF basisphenoid fossa; CF condyloid foramen; CFO condyloid fossa; DC dorsal crest; ETG epitympanic groove; ETR epitympanic recess; F frontal; FB basicochlear fissure; FEO oval window; FER round window; FM foramen magnum; FO foramen ovale; FOR foramen; G glenoid; IA incisor alveolus; IF infraorbital foramen; IOS interorbital sinus; IP interparietal; J jugal; JF jugular foramen; LC lambdoidal crest; LF lacrimal foramen; M mastoid; M¹ first molar; MF maxillary fossa; MX maxilla; N nasal; OC occipital condyle; OF optic foramen; P periotic; PA parietal; PGP postglenoid process; PGP postglenoid process; PL palatine; PM premaxilla; PMP premaxillary process; POP paroccipital process; PP posterior process; PR promontorium; PS presphenoid; PT pterygoid; PTP post-tympanic process; PY pyriform fenestra; SC sagittal crest; SEC semicircular canals; SF sphenorbital fissure; SMF supraorbital ridge; SO supraoccipital; SQ squamosal; SR supraorbital ridge; SVII sulcus for facial nerve (VII). Bar indicates 5mm.

missing. The posterior edge of the pterygoid wing curves ventrally and posteriorly and slightly medially before forming a second, laterally-directed flange.

Zygomatic arch. The ventral margin of the zygomatic arch is slightly arched and lies dorsal to

the tooth row. Anteriorly, the dorsal margin sinks in the jugal region then, posteriorly, rises at an angle of approximately 45 degrees to the ventral surface to form the very tall squamosal projection. The latter rises to at least the level of the dorsal edge of the infraorbital foramen. Its maximum height occurs dorsal to the glenoid surface. A masseteric scar occurs on the anterolateral ventral surface of the arch. In dorsal view, the junction between the zygomatic arch and its anterior extension onto the face is marked by a change in direction of the arch from posterolateral (anteriorly) to posterior, the anterior extensions diverging far more than the zygomatic arches proper. The latter appear to have been almost parallel for much of their length.

Cranial vault. The braincase is widest at the level of the post-tympanic processes, narrowest in the interorbital area and highest dorsal to the postglenoid processes. There is little development of the lambdoidal crests and no nuchal crest so that the braincase is rounded at its posterior extremity in lateral and dorsal views. The sagittal crest is variably developed (perhaps reflecting sexual dimorphism). Where it occurs, the sagittal crest is low and extends anteriorly to the supraorbital ridges and posteriorly to the interparietal at a point dorsal to the paroccipital processes. Approximately two-thirds along the length of the braincase, within the parietals, are bilaterally depressed areas that mark a conspicuous venous sinus. Its trajectory is easily traced in a lateral then anterolateral direction before it opens to the exterior in the posterior part of the postglenoid foramen. Along the sinus several small orifices open to the exterior.

Glenoid. The glenoid surface is only slightly concave and is subcircular, being almost as long as wide. It ends medial to the zygomatic process of the squamosal. The postglenoid process is weak. In height it is less than one quarter the length of the glenoid surface; its anterior face is not noticeably anteriorly recurved. The large postglenoid foramen opens vertically on the steeply sloping posterior face of the glenoid, giving the opening an elliptical shape. It opens immediately posterior to the postglenoid process. Medial to the glenoid surface, the foramen ovale opens in the alisphenoid on the side of a bony prominence or ridge. The latter separates the ventrally opening foramen ovale from a second, more posterodorsal and lateral foramen that opens posterolaterally (i.e. into the pyriform fenestra).

Temporal region. Posterior to the glenoid region and immediately anterior to the mastoid

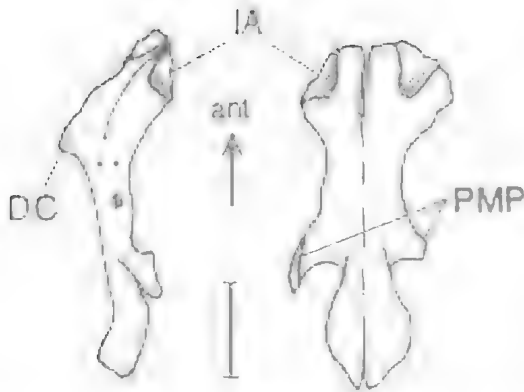


FIG. 4. *Hipposideros* (*Bruchipposideros*) *nooraleebus*. Microsite, Riversleigh Station. QMF19044, left ventral view; right lateral view. Bar indicates 1mm.

region, the post-tympanic process of the squamosal is developed with a vertical process that forms a slim posteromedially directed point. In lateral view, the posteroventral part of the lateral face of the petiotic is exposed and the round window visible. In the otic region, the squamosal swells slightly laterally and circumscribes an indentation which would have accommodated the tympanic ring. The squamosal laterally and anterolaterally, the alisphenoid anteriorly and the basisphenoid medially, contribute to the anterior edge of the cavity occupied by the petiotic. At the anterolateral corner of the tympanic cavity, the pyriform fenestra forms a broad gap separating the posterior face of the glenoid from the anterolateral wall of the petiotic. The posterolateral wall of the skull is deeply notched between the post-tympanic process of the squamosal and the paroccipital process. This notch is filled by the mastoid.

Basicranium. The medial sphenoid series (basisphenoid and presphenoid) is broadly fused with the palatine, pterygoid, alisphenoid and basioccipital. The basisphenoid appears relatively flat in its central region or perhaps only slightly concave. Faint, anteriorly convergent ridges define the basisphenoid fossa (and mark the boundary between the pterygoid and basisphenoid anteriorly and probably the alisphenoid and basisphenoid posteriorly). The petiotics are not enlarged, their width being about twice the shortest distance between the two. Thus the lateral edges of the basisphenoid-basioccipital complex are relatively straight with only shallow biconcave lateral curves. The anterior margin of the basicranial area is not preserved. The petiotic is bordered medially and posteriorly by the

basioccipital. Anteromedially, the basisphenoid abuts the petiotic; there is no lateral extension of the basisphenoid or medial extension of the petrosal.

Occipital. The most posterior region of the skull coincides with the junction of the interparietal and supraoccipitals. In lateral view, the supraoccipital is not very convex posteriorly but the exoccipitals nonetheless overhang the posteroventrally directed foramen magnum. The posterior edge of the foramen magnum is straight and not thickened. There is little development of the lambdoidal crests but a distinct ridge marks the junction of the interparietal and supraoccipitals. It parallels the posterior edge of the foramen magnum, terminating anteriorly in the region dorsal and lateral to the paroccipital process, i.e. immediately to the rear of the mastoid region. A supramastoid foramen opens on the occipital surface dorsal to the ventral condyloid fossa. There are no parietal crests and no posteriorly directed point on the skull: the nuchal line continues smoothly over the top of the skull.

In ventral view, the posterior skull contour of the supraoccipital at the level of the lambdoidal ridge is rounded. The foramen magnum is oval in shape and wider than high. Between the occipital condyle and paroccipital process is a deep condyloid fossa. The paroccipital process is well developed and forms the lateral-most part of the occipital bone. The tip is not preserved but the process appears to have articulated with the mastoid. The condyle projects most strongly ventrally at the posterior extremity, its thickened lip partially concealing the condyloid foramen in the anterolateral face.

Ear region. The ectotympanics and auditory ossicles are missing. The petiotic is only weakly articulated with the surrounding basicranial elements and exhibits the condition described by Novacek (1991) as 'phanerocochlear' found in most adult microchiropterans. In this species, attachment of the petiotic appears to be solely via connective tissue although the petiotic closely abuts the basicranial elements medially via the basisphenoid-occipital complex and laterally via the post-tympanic process of the squamosal and the paroccipital process. The anterior part of the middle ear cavity is unossified as a pyriform fenestra which is a restricted opening between the petiotic and the squamosal and most posterolateral part of the alisphenoid. There is little development of an epitympanic recess or ectotympanic groove, the bone here being no thicker than the squamosal that bounds it. Posteriorly, the large

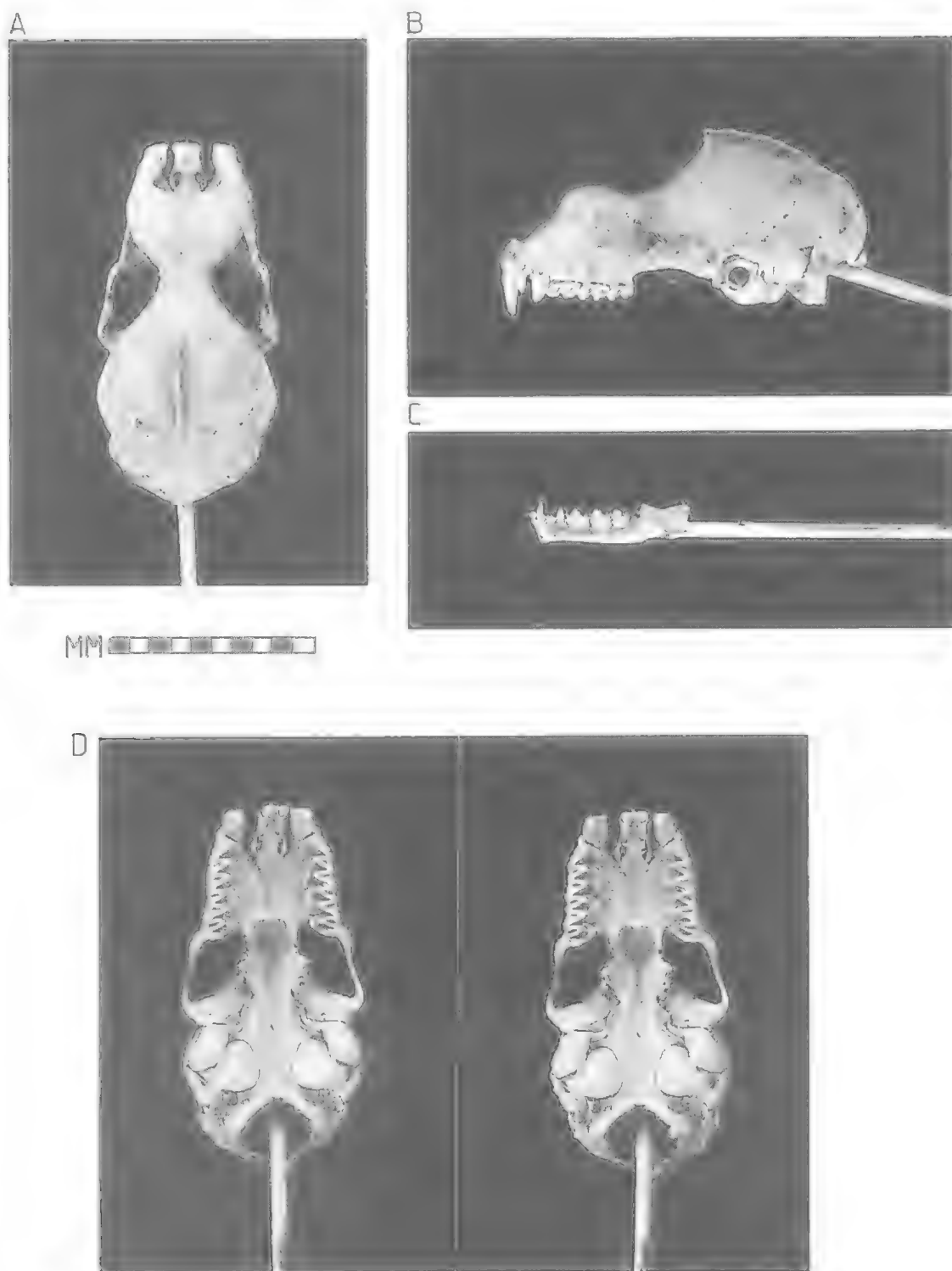


FIG. 5. *Rhinonictes aurantius*, AR15400, Klondyke Queen Mine, Marble Bar, Western Australia. A, skull dorsal view; B, skull lateral view; C, jaw lateral view; D, skull ventral view, stereopair. Scale in mm.

jugular foramen and the more medial, very narrow basicochlear fissure are coalescent.

In ventral view, the cochlear labyrinth is visible through the thin bone of the promontorium so that the petrosal has a snail-like appearance. Three turns of the labyrinth can be detected through the bone and this is confirmed by examination of sectioned periotics.

In the lateral face of the periotic the following structures are visible. Most posteriorly, above the ventral plane of the basioccipital and facing the jugular foramen, is the aqueductus cochleae. Lateral and ventral to this, at the posterolateral corner of the periotic and distinct in ventral view, is the round window, a large, flattened oval orifice. More anteriorly and dorsally, the oval window is slightly more elongate. A very slight transverse groove, barely imprinted on the promontorium medial to the round and oval windows, marks the passage of the stapedial artery, a branch of the internal carotid. Lateral to the round and oval windows, and at the base of the promontorium, is a deep, elongate, curved depression or canal which dips from front to rear. This is the canal for the facial nerve (VII). The canal terminates posteriorly a little anterior to the round window in the region of the stapedial fossa and continues anteriorly beyond the oval window via an orifice (the apertura tympanica canalis facialis).

The lateral margin of the canal is a vertical, curved face. Anteriorly, a small process (the anterior process of the petrosal; Henson, 1970) protrudes anteromedially into the pyriform fenestra. It does not articulate with the squamosal. Near its base is a small foramen (possibly for the superior ramus of the stapedial artery). Behind this process the lateral edge of the periotic curves back and dorsal and is appressed closely to the squamosal. Immediately medial to the post-tympanic process, the lateral edge terminates in a prominent process (posterior process of the petrosal; Henson, 1970) that overhangs the stapedial fossa.

The mastoid occupies a lateral, posterior and dorsal position in the periotic. The mastoid wall only thinly covers the three semicircular canals.

Incisors. The dentition of *B. nooraleebus* has been described previously by Sigé et al. (1982), except for the incisors which are now known as follows. There is one pair of upper incisors, I¹, and two pairs of lower incisors, I₁ 2. The upper incisors are bilobed with the outer lobe slightly wider but shorter than the inner lobe. The lower incisors are tricuspidate and I₁ is smaller than I₂.

COMPARISONS

RHINONICTERIS AURANTIUS

The skull of *B. nooraleebus* is smaller than that of *R. aurantius* (Gray, 1847) (AR17573, M8416, AR15400; Fig. 5) being approximately three quarters its size. Its shape is generally similar but differs as follows. The rostrum is lower in *R. aurantius* and has less prominent inflations. The trough separating the rostral inflations is deeper and narrower, poorly delimited by supraorbital ridges and is perforated by tiny foramina. The bar of bone that extends the zygomatic arch anteriorly onto the face, and encloses the infraorbital foramen, is directed dorsally (i.e. vertically) then anterodorsally so that it appears much more convex.

The postpalatal foramen is much smaller in *R. aurantius* and is surrounded by many small foramina. Dorsal and medial to this, there is one foramen (rather than two) opening into a groove. In general, unlike *B. nooraleebus*, the skull of *Rhinonictoris* is perforated by many tiny foramina, particularly in the interorbital and pterygoid regions. The palates are similar. The premaxillae are strikingly similar except that in *R. aurantius* the anterior premaxillary processes completely enclose the anterior palatal foramina. The premaxillae of both taxa exhibit a very distinctive dorsal crest as well as a dorsal convexity that results in the incisors being directed ventrally rather than anteriorly.

The sagittal crest is quite different. In *R. aurantius* it is tall and originates abruptly (with an anteriorly curved point) at the highest point of the skull (i.e. dorsal to the postglenoid process) and does not extend as far posteriorly. The vertical projection of the zygomatic arch is possibly taller and extends further anteriorly, involving the jugal and hence most of the zygomatic length. The lambdoidal crests are better developed (especially laterally) giving the posterior margin of the braincase a squared rather than rounded appearance. The postglenoid process is better developed (being more curved) and the pterygoid region less constricted. Ridges defining the basisphenoid fossa are weak and almost parallel (rather than convergent). The postglenoid foramen is elliptical and proportionately smaller. The dorsal margin of the foramen magnum is indented.

The ear region is very similar in the two taxa. The general orientation and attachment of the periotic to surrounding basicranial elements is similar and periotic morphology very similar. In the periotic the bony wing developed lateral to the

anterior and posterior processes is not as well developed.

As described by Sigé et al. (1982), C^1 of *R. aurantius* has a better developed secondary cusp and less developed cingulum, and there is more expansion of the heel on M^2 . The dentaries are similar. In both taxa the horizontal ramus is short and slender with a chin process, the coronoid process is very low (the tip only exceeding the molar heights by a molar crown height or less) and the masseteric fossa has a very expanded, almost horizontal border which extends posteriorly into a wide, rounded angular process that is buccally markedly extended.

HIPPOSIDEROS (HIPPOSIDEROS) SPEORIS

The skull of *H. speoris* (Schneider, 1800) (M3468; Fig. 6) is described in so far as it differs from both *B. nooraleebus* and *R. aurantius* except where specifically stated. It is similar in size to *R. aurantius* and approximately one-third larger than *B. nooraleebus*. The rostrum is proportionately narrower, the braincase wider and the rostral inflations, and trough separating them, less conspicuous. The posterior trough is also shallower. The supraorbital ridges are much better defined laterally (being less attenuated by inflations). The facial portion of the skull slopes posterodorsally more gradually. The bar of bone anteriorly extending the zygomatic arch onto the face is directed anterodorsally and is straight (or even concave) rather than convex. The infraorbital foramen occurs above M^1 rather than M^2 and is lower on the face. The lacrimal foramen is larger (than in *R. aurantius* at least) and the ventral fossa much broader and alveolar foramina more conspicuous than in *B. nooraleebus* and *R. aurantius*. More of the lateral face is visible (i.e. the bar of bone hides less) and a third foramen, occurring dorsal and posterior to the lacrimal, is visible on the lateral wall of the rostrum.

There appear to be two foramina posterior to the palate (the more lateral one perhaps being homologous to the postpalatal foramen observed in *B. nooraleebus*). Unlike *B. nooraleebus* but like *R. aurantius*, the skull is perforated by many tiny foramina especially in the interorbital region, where, for example, many open into the interorbital sinus. Note that although the sinus is present in the three taxa examined it has a different form in each. The sphenoidal fissure is relatively shorter perhaps because the skull proportions differ. Compared to *R. aurantius*, the braincase of *H. speoris* is relatively longer and the interorbital region shorter.

The palate differs in that the tooththrows are anteriorly convergent, the posterolateral indentations extend to the the posterior faces of M^2 and the posteromedial palate is marked by an indentation rather than a spine. There are many tiny palatal foramina but most pronounced are a pair of foramina medial to the anterior faces of M^2 and the anterior limits of the lateral indentations (i.e. medial to the posterior faces of M^2). In the premaxillae, the processes only partially enclose the anterior palatal foramina (these processes appear to diverge posteriorly), there is no dorsal crest, little lateral convexity and the incisors are directed anteriorly. The supraorbital ridges unite at the level of the narrowest constriction in the interorbital region rather than posterior to it.

The pterygoids are more constricted and there is no second flange on the pterygoid wing. The squamosal projection of the zygoma is much less well developed. In *H. speoris* it rises from approximately halfway along the zygomatic arch to quickly reach its maximum height (level with the dorsal margin of the ectotympanic ring). In *R. aurantius* it arises further anteriorly, so that its development involves almost the entire length of the zygomatic arch, to more gradually reach at least twice this height. (Note that there may be some variation in the height and shape of this projection in *R. aurantius*: cf. AR15400 and AR17573.) In both, however, the maximum height of the projection is reached at a point above the glenoid surface. In *R. aurantius* the projection leans dorsomedially towards the braincase; it is vertical in *H. speoris*.

The braincase narrows immediately anterior to the post-tympanic process rather than anterior to the postglenoid process. Like *B. nooraleebus* but unlike *R. aurantius*, there is little development of the lambdoidal crests so that the posterior margin of the skull appears rounded. The sagittal crest is similar to *B. nooraleebus* but the latter extends further posteriorly. The postglenoid process is better developed than in *B. nooraleebus* and *R. aurantius*. The articulating surface is wider; it is oval rather than subcircular. The postglenoid foramen is small and circular rather than large and oval. Dorsally and posteriorly are a number of tiny foramina which vary in number, size and position from one side of the skull to the other.

Medial to the glenoid surface are a number of foramina, the largest and most medial presumably being the foramen ovale. The sphenoid complex is concave rather than flat and the lateral margins of the basisphenoid-occipital more concave than in *B. nooraleebus* and much more so

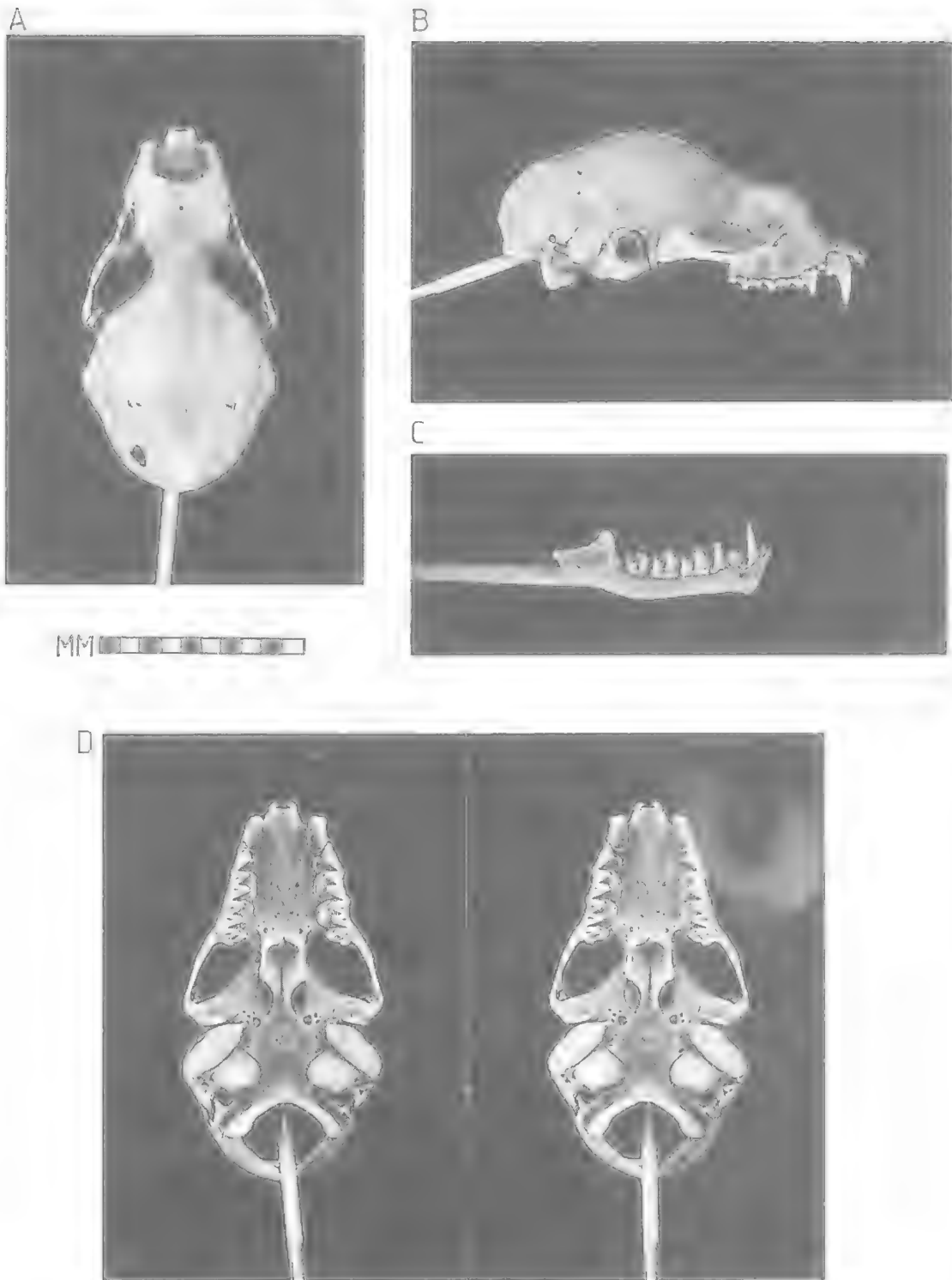


FIG. 6. *Hipposideros speoris speoris*, M3468, Kalutara, Sri Lanka. A, skull dorsal view; B, skull lateral view; C, jaw lateral view; D, skull ventral view, stereopair. Scale in mm.

than in *R. aurantius*. There is a lateral extension of the basisphenoid over the anteromedial corner of the periotic and foramina occur at the most lateral point of the extension. As in *B. nooraleebus*, the dorsal margin of the foramen magnum is straight. The foramen magnum is oval, being conspicuously wider than long. The junction of the interparietal and supraoccipitals terminates laterally at the paroccipital process (rather than dorsolateral to it). Differentiation of the jugular foramen and basicochlear fissure is less conspicuous (i.e. their coalescence is more gradual) due to the different shape of the occipital (i.e. its lack of an extra wing). The paroccipital process articulates with the mastoid and squamosal. The notch between the paroccipital process and post-tympanic process is shallower (i.e. is filled in more posterodorsally by the squamosal and the supramastoid foramen is round rather than triangular in lateral view).

Attachment of the periotic to surrounding basicranial elements differs. The periotic abuts the basisphenoid anteromedially rather than medially and the basisphenoid extends onto the anterior promontorium. The basicochlear fissure is located medially and posteromedially and is much larger and more coalescent with the jugular foramen. The anterolateral face of the periotic is flattened. The anterior process of the periotic probably abuts the squamosal which contributes to the better-developed epitympanic recess. The pyriform fenestra appears to be narrower.

In *H. speoris*, I^1 has a reduced outer lobe, C^1 has a less developed secondary cusp and cingulum, P^2 is slightly less buccally extruded from the tooth row than in *B. nooraleebus*, M^2 heel less expanded, and M^3 more reduced such that it is narrower and shorter and the premetacrista is shorter. The coronoid process of the dentary is not as low and the angular process is narrower and extends more posterobuccally than buccally. The lower incisors protrude anteriorly, C_1 is relatively tall, P_2 small and M_3 more reduced (shorter and narrower but with a hypoconulid).

DISCUSSION

The Old World tropical to subtropical bat family Hipposideridae contains sixty-plus living species referred to the genus *Hipposideros* (approximately 50 species) and eight other genera (of one to two species each) including *Rhinonictis*, *Coelops*, *Triaenops*, *Cloeotis*, *Asellia* and *Aselliscus* (Hill & Smith, 1984). Tertiary-aged hipposiderids, which have been recovered

from mainly karstic sediments in Europe, Africa and Australia, are referred to the genera *Palaeophyllophora*, *Asellia* and the subgenera *Hipposideros* (*Pseudorhinolophus*) Schlosser, 1887 (late Eocene-middle Miocene taxa), *Hipposideros* (*Brachhipposideros*) Sigé, 1968 (late Oligocene-middle Miocene taxa) and *Hipposideros* (*Syndesmotis*) Peters, 1871 (middle Miocene-Recent taxa). *Hipposideros* (*Hipposideros*) has generally been reserved (e.g. by Sigé, 1968) for Recent hipposiderid species.

Riversleigh's *Brachhipposideros nooraleebus* is known from thousands of specimens and dominates the vertebrate fauna of Microsite. All other vertebrate taxa in the deposit are known from at most a few specimens each. Microsite is the only Riversleigh fossil deposit dominated by a single bat species. Because of this, it has been possible to refer incomplete hipposiderid cranial material collected from Microsite to the single taxon *Brachhipposideros nooraleebus*. Most of Riversleigh's other 150-plus Oligo-Miocene fossil vertebrate deposits contain between three and ten microchiropteran taxa (see Archer et al., 1991). French fossil faunas containing *Brachhipposideros* species also commonly contain more than one hipposiderid taxon and no skull material referable to a species of *Brachhipposideros* has previously been described.

In the present study, the skull of *H. (B.) nooraleebus* has been compared with the skulls of a modern representative of the genus *Hipposideros*, the type species *Hipposideros speoris* of India and Sri Lanka; and a probable Recent descendant of the Australian *Brachhipposideros* lineage, *Rhinonictis aurantius* (Sigé et al., 1982).

Many striking differences distinguish *H. (B.) nooraleebus* from its congener *H. (H.) speoris*. In particular, differences were observed in: overall skull proportions; rostral morphology, including the size and position of the infraorbital and lacrimal foramina and maxillary fossa; morphology of the palate, premaxilla and zygomatic arch; attachment of the periotic to the surrounding basicranial elements; squamosal articulation with the paroccipital process; and, in the dentition, the reduced M_3 s, I^1 with reduced outer lobe, M^2 with less expanded heel, tall C_1 and small P_2 . Similarities between the two skulls include the form of the sagittal crest and general shape of the braincase.

On the other hand, the skull of *H. (B.) nooraleebus* appears to be very similar in overall form to that of *R. aurantius*. Similarities include the general proportions of the skull, the broad rostrum,

subparallel tooth rows, morphology of the palate and zygomatic arch, the crested premaxillae, general basicranial morphology, very similar periotic and otic morphology, the pronounced accessory cusp on C^1 and little reduced upper and lower M3s. Obvious differences occur in the shape of the braincase and form of the sagittal crest.

In his study of the phyletic relationships of fossil hipposiderids, Legendre (1982) recognised that *Hipposideros* probably represents a paraphyletic group (see also Sigé, 1968) and that current taxonomy does not accurately reflect understanding about the evolutionary relationships of its supraspecific groups. Species of *Brachiposideros* have been recognised to have special affinities with small Recent species of *Hipposideros* (e.g. *H. caffer*), *Syndesmotis* and *Rhinonycteris* (Sigé, 1968; Legendre, 1982; Sigé et al., 1982). Those of *Pseudorhinolophus* appear to have affinities with species of *Asellia* and some large Recent *Hipposideros* species (e.g. *H. armiger*, *H. diadema* and *H. commersoni*) (Hugueney, 1965; Sigé, 1968; Legendre, 1982).

To refine understanding about the relationships of *Brachiposideros nooraleebus* to *Rhinonycteris aurantius* and other hipposiderids, further comparisons of skull and postcranial morphology of many additional hipposiderid groups are required. Pending this much larger study, comparisons made here support Sigé et al.'s (1982) hypothesis that the Australian taxa *B. nooraleebus* and *R. aurantius* are closely related.

ACKNOWLEDGEMENTS

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NIMBADON, A NEW GENUS AND THREE NEW SPECIES OF TERTIARY
ZYGOMATURINES (MARSUPIALIA: DIPROTODONTIDAE) FROM NORTHERN
AUSTRALIA, WITH A REASSESSMENT OF *NEOHELOS*

S. J. HAND, M. ARCHER, H. GODTHELP, T.H. RICH AND N.S. PLEDGE

Hand, S.J., Archer, M., Godthelp, H., Rich, T.H. & Pledge, N. S. 1993 06 30: *Nimbadon*, a new genus and three new species of Tertiary zygomaturines (Marsupialia: Diprotodontidae) from northern Australia, with a reassessment of *Neohelos*. *Memoirs of the Queensland Museum* 33(1): 193-210. Brisbane. ISSN 0079-8835.

Three new species of Oligo-Miocene zygomaturine diprotodontids are described from northern Australia. All are small, plesiomorphic and appear to comprise a distinctive clade of zygomaturines, named here *Nimbadon*. The clade is partly defined on the basis of the posteriorly inclined P³ parastyle and blade extending from the parametacone to the lingual half of the P³ crown and then to the anterolingual cingulum. Two of the species are known from Oligo-Miocene local faunas of Riversleigh Station, northwestern Queensland. The third is from the middle Miocene Bullock Creek Local Fauna of Camfield Station, northwestern Northern Territory. Description of additional fossil material referable to *Neohelos tirarensis* Stirton, 1967, a middle Miocene zygomaturine from the Kutjamarpu Local Fauna of South Australia, enables the genus to be distinguished from *Nimbadon*. The chronostratigraphic significance of the new zygomaturines is considered and found to approximately correspond to current understanding of the relative ages of the deposits from which the specimens were obtained. □ *Diprotodontidae*, *Zygomaturinae*, *Nimbadon*, *Neohelos*, *Oligo-Miocene*, *Riversleigh*, *Bullock Creek Local Fauna*, *Henk's Hollow Local Fauna*, *Fig Tree Local Fauna*.

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Specimens representing a very small zygomaturine were collected between 1984 and 1986 by Archer, Godthelp and Hand from the Henk's Hollow Site, in an as yet unnamed freshwater limestone on the Gag Plateau of Riversleigh Station (Archer, Hand & Godthelp, 1986; Archer & Flannery, 1987; Archer et al., 1989, 1991). Referred material includes maxillary and dentary fragments and isolated teeth. A second, larger Riversleigh species, represented by a maxilla, was collected in 1986 by Pledge from Fig Tree Site Locality adjacent to Godthelp Hill, Riversleigh Station.

A small Bullock Creek zygomaturine is known from a palate collected in 1981, by Rich and colleagues, from Horseshoe West Locality (WV 113) in the Camfield Beds of Camfield Station, northwestern Northern Territory (Rich et al., 1982, 1991).

Estimates of the age of the Henk's Hollow, Fig Tree and Bullock Creek Local Faunas are based mainly on stage-of-evolution comparisons of particular diprotodontian marsupials with those of other northern and central Australian faunas

(Rich et al., 1982, 1991; Archer & Flannery, 1983; Archer & Hand, 1984; Woodburne et al., 1985; Murray, 1990a; Murray & Megirian, 1990; Archer et al., 1989, 1991). Recent reappraisal of the age of central Australian Tertiary mammalian faunas, based on the study of foraminifera (Lindsay, 1987), suggests that some of these faunas (e.g. the Ditjimanka, Pinpa and Ericmas Local Faunas) are appreciably older than once thought (e.g. Woodburne et al., 1985; but see Tedford, 1966), possibly late Oligocene. By comparison, the Bullock Creek Local Fauna is estimated to be ?middle Miocene in age, i.e. immediately post-Wipajiri (Murray, 1990a; Murray & Megirian, 1990). On-going studies (Archer et al., 1991) of the Riversleigh fossil faunas suggest that the Henk's Hollow Local Fauna is ?middle Miocene in age and the Fig Tree Local Fauna somewhere between late Oligocene and early Miocene in age.

The new zygomaturines described here are most similar to forms currently referred to the genus *Neohelos*. Their generic distinction, however, has been clarified by discovery at the type locality of new material referable to *Neohelos*

TABLE 1. Measurements of *Neohelos tirarensis* P³ (AMF87625) and M³ (AMF87626) from the Leaf Locality, Lake Ngapakaldi, South Australia. In mm. Abbreviations: ant, anterior; post, posterior; paramet, parametacone; protoc, protocone; parac, paracone.

P ³	Length	15.8
	width	13.9
	width(paramet to protoc tips)	5.5
	height(paramet)	11.4
	height(parastyle)	6.5
M ³	length	18.8
	width(ant)	17.2
	width(post)	15.8
	height(parac)	7.8

tirarensis, the type and only named species of the genus. The original description (Stirton, 1967) of this Miocene zygomaticurine from the Kutjamarpu Local Fauna of central Australia was based on five isolated teeth collected in 1962 at the Leaf Locality, Lake Ngapakaldi, Etadunna Station, South Australia. The holotype, a broken P³, preserves only the posterior portion of the tooth. Though less complete than the other teeth, it was selected as the holotype because of the importance of premolar morphology in diprotodontoid systematics (Stirton, 1967; Stirton, Woodburne & Plane, 1967).

In 1982 two isolated teeth referable to *N. tirarensis* were collected from the type locality by Archer, Hand, T. Flannery, G. Hickie, J. Case and P. Bridge: a well-preserved RP³ (AMF87625) and RM³ (AMF87626). These add considerably to knowledge of this species. Additional materials referable to *Neohelos* from the Bullock Creek Local Fauna (Plane & Gatehouse, 1968; Plane, 1971; Murray & Megirian, 1992) and various Oligo-Miocene Riversleigh local faunas (Archer et al., 1989, 1991) are presently under study.

Institutional abbreviations used here are as follows: QMF, fossil collection of the Queensland Museum; AMF, fossil collection of the Australian Museum; SAMP, palaeontological collection of the South Australian Museum; NMVP, palaeontological collection of the Museum of Victoria; AR, research collection of the School of Biological Sciences, University of New South Wales. Cusp nomenclature follows Archer (1984) and Rich, Archer & Tedford (1978). The posterolingual cusp of the upper molars, conventionally called the hypocone (e.g. Stirton, Woodburne & Plane, 1967), is now called the metaconule following Tedford & Woodburne (1987) but the posterolingual cusp of P³, follow-

ing unchallenged convention, is called the hypocone. Cheektooth homology is that proposed by Archer (1978). Higher level systematic nomenclature follows Aplin & Archer (1987).

SYSTEMATICS

Superorder MARSUPIALIA Illiger, 1811
Order DIPROTODONTIA Owen, 1866
Family DIPROTODONTIDAE Gill, 1872
Subfamily ZYGOMATURINAE Stirton,
Woodburne & Plane, 1967

Neohelos Stirton, 1967
(Fig. 1, Table 1)

Type species. Neohelos tirarensis Stirton, 1967

REVISED GENERIC DIAGNOSIS

The following combination of features appears to distinguish species of *Neohelos* from all other zygomaticurines: P³ with large, erect parastyle that is well isolated from the parametacone; parastyle is conical without tip developed as a blade; anterolingual basin well defined in P³ by distinct basal cingulum extending between parastylar corner of tooth to anterolingual base of protocone; P³ parametacone with an undivided tip; parametacone tip not developed into anterobuccally oriented blade; line between protocone, parametacone and widest buccal point on crown is approximately rectilinear and divides crown either in half or leaves anterior division shorter than the posterior division; P³ with well-developed hypocone or hypocone shelf; M²⁻³ with well developed parastyle and metastyle.

Nimbador n.gen.
(Figs 2-5, Table 2)

Type species. Nimbador lavarackorum n.sp.

Additional species. Nimbador whitelawi n.sp., *Nimbador scottorum* n.sp.

GENERIC DIAGNOSIS

Species of *Nimbador* differ from those of all other zygomaticurines (with special reference to *Neohelos*, the taxon to which they are otherwise most similar) in the following combination of features: small size (although they are larger than *Raemotherium* Rich, Archer & Tedford, 1978); in having a molar gradient that does not appreciably increase posteriorly (in contrast to all other zygomaticurines except *Raemotherium*); posteriorly inclined parastyle on P³ (rather than conical

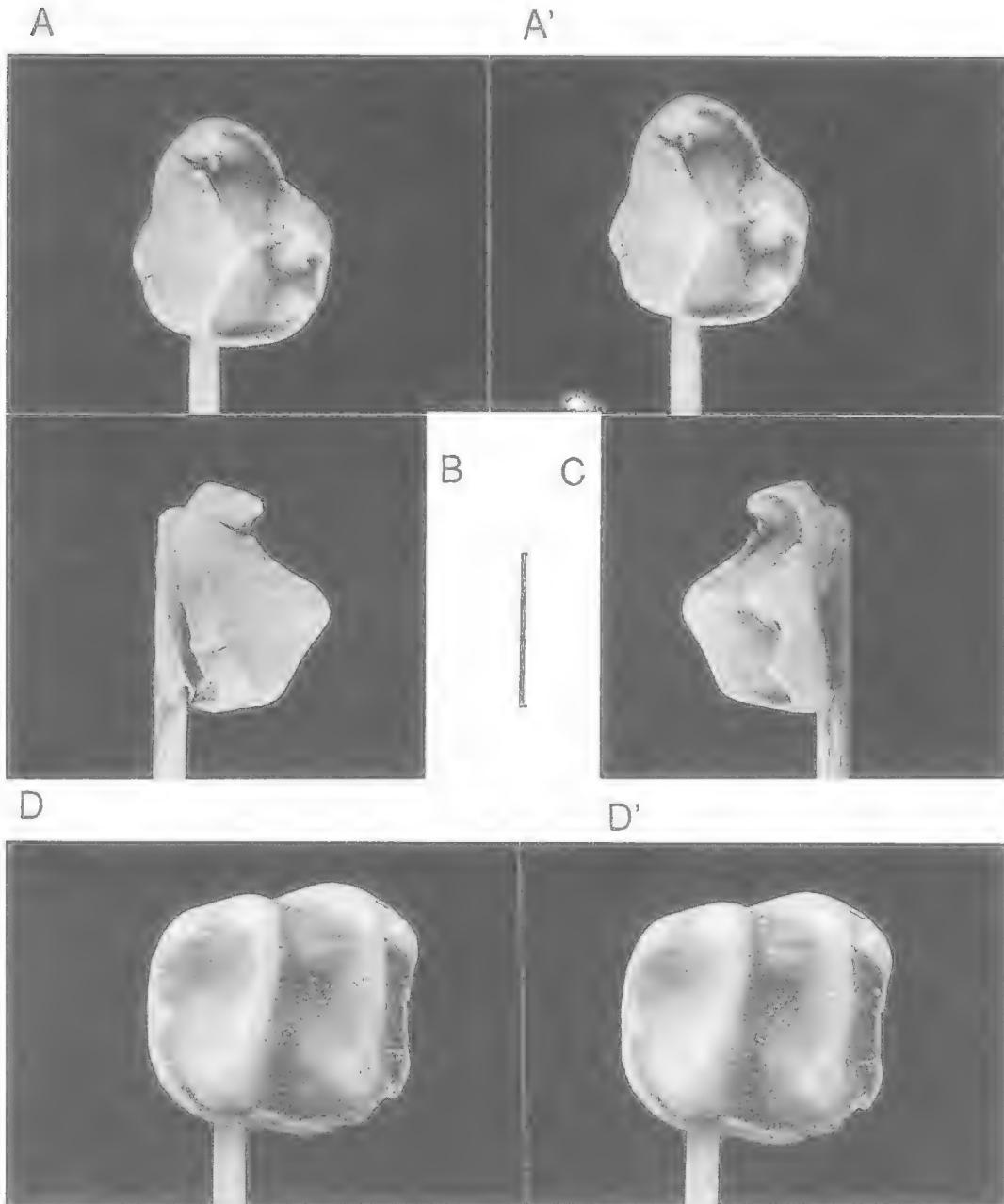


FIG. 1. *Neohelos tirarensis*, Leaf Locality, Lake Ngapakaldi, South Australia. AMF87625, RP^3 : A-A', occlusal stereopair; B, buccal view; C, lingual view. AMF87626, RM^3 : D-D', occlusal stereopair. Bar indicates 10mm.

and erect as in other zygomaturines except possibly *Plaisiodon centralis* Woodburne, 1967); an anterolingual blade on the parastyle of P^3 that surmounts a posterolingually oriented thegotic facette (in contrast to no apical blade such as may[?] characterise *Neohelos*); completely undivided parametacone on P^3 (in contrast to all other

zygomaturines except *Neohelos* and *Alkwertatherium* Murray, 1990b); an anterobuccal blade on the parametacone of P^3 that surmounts an obliquely oriented anterolingual thegotic facette (in contrast to either no blade or a poorly developed anteriorly oriented blade such as may[?] characterise *Neohelos*); very small to absent hy-

CENTER DENTITION												N. whitelawi		N. scottorum	
Species		Nimbadon lavarackorum										NVM P186506		23157	
QMF		23141	23143	23144	23145	23146	23147	23148	23149	23150	23160*	right	left		
P ³	L	12.7	14.1	12.4								12.9	13.0	14.3	
	w			10.3								(10.4)	10.9	13.4	
M ²	L	11.9			13.3						14.1	13.1	13.2	17.1	
	w(ant)	10.2			10.9						11.3	(9.3)		15.0	
	w(post)	9.9			10.8						10.5	9.2		15.8	
M ³	L	12.3				13.7					14.3	13.1		17.9	
	w(ant)	11.3									11.6	10.9			
	w(post)	10.1				10.9					10.4	(9.5)			
M ⁴	L						13.8		14.3			13.5		18.5	
	w(ant)						11.5		12.2			11.1			
	w(post)						10.7	12.5	10.4			9.7			
M ⁵	L									13.5				18.1	
	w(ant)									11.3					
	w(post)									9.8					
Palate width												29.2			
P ³ -M ⁵	L													(84.4)	
P ³ -M ⁴	L											52.8		66.3	
P ³ -M ²	L											25.3	25.8	48.2	
M ²⁻⁵	L													(71.5)	
M ^{2-nl}	L											39.5		53.1	

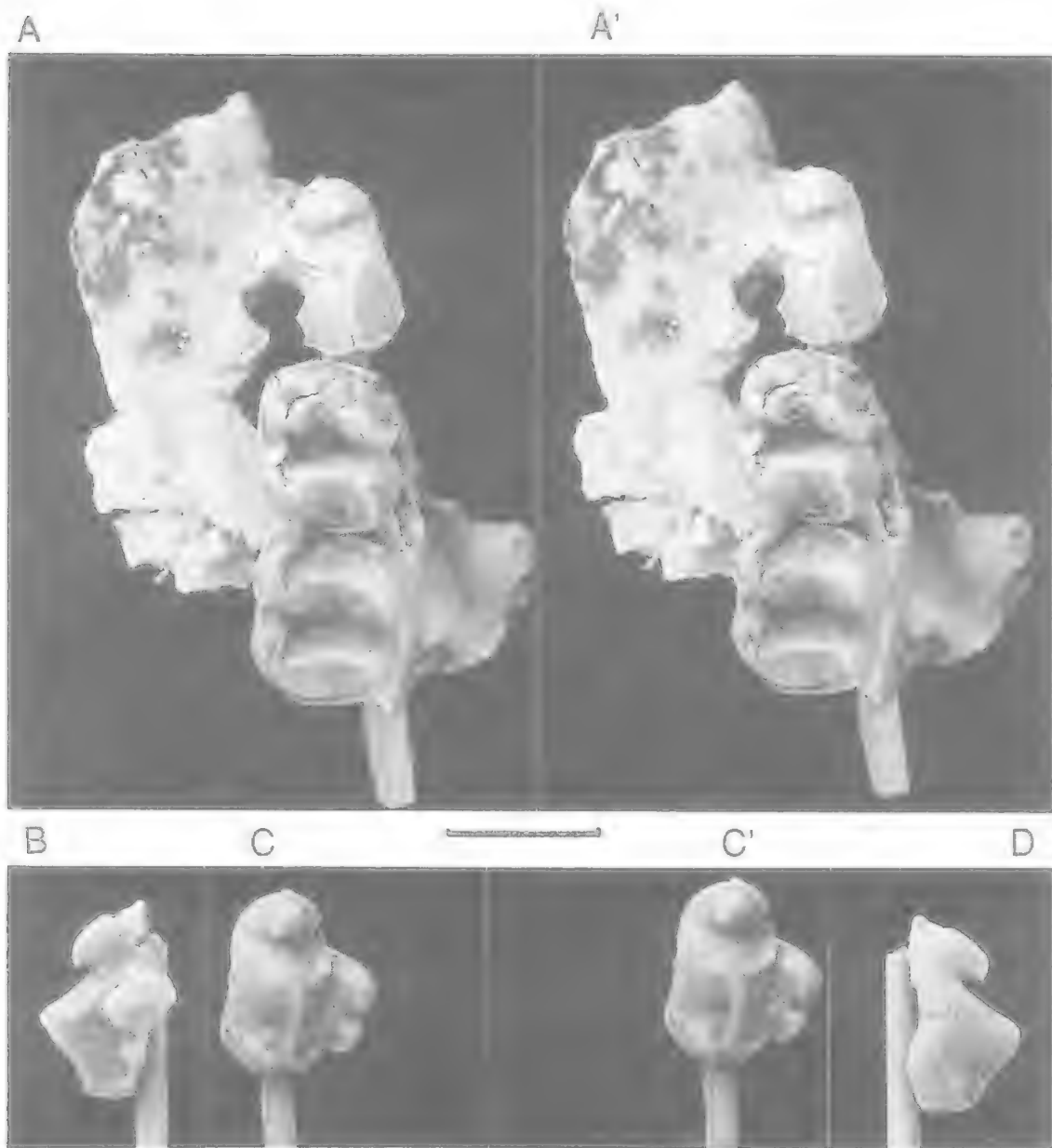


FIG. 2. *Nimbadon lavarackorum* n.gen., n.sp., Henk's Hollow Site, Riversleigh Station. A A', QMF23141, holotype, left maxillary fragment with M^2 , M^3 and buccal half of P^3 , occlusal stereopair. B-D, QMF23143, RP^3 : B, lingual view; C-C', occlusal stereopair; D, buccal view. Bar indicates 10mm.

pocone on P^3 (in contrast to *Alkwertatherium* and most but not all *Neohelos* and in contrast to all other zygomaticurine P^3 s where this cusp is large, including *Maokopia* Flannery, 1992); posterobuccal basal cingulum on P^3 (in contrast to most other zygomaticurines except *Alkwertatherium* and *Neohelos* where this feature is variably

developed); poorly developed to absent anterolingual basal cingulum joining base of parastyle to base of protocone (in contrast to most other zygomaticurines except some *Neohelos* where there may be only a very small cingulum); an anterolingual crest on P^3 that extends from the parametacone towards the protocone but, veering

anteriorly, bypasses the buccal crest from the protocone and extends to the anterolingual basal cingulum (in contrast to directly connecting to the buccal crest from the protocone as occurs in most if not all other zygomaturines); a line extended buccally through the protocone and parametacone passes anterior to the position of the widest point on the buccal base of the crown (in contrast to intersecting this point as it does in *Neohelos* and *Alkwertatherium*, although this feature is variable in *Nimbadon whitelawi* n.sp.); this same line divides the crown such that the anterior moiety is longer than the posterior one (as it does in *Alkwertatherium* but in contrast to either dividing the crown into approximately equal lengths or into shorter anterior and longer posterior moieties as it does in *Neohelos*); poorly developed parastyles and metastyles on upper molars (in contrast to species of *Neohelos* but as in some anterior teeth of other zygomaturines such as *P. centralis*).

ETYMOLOGY

Nimba is a northwestern Queensland Aboriginal word (Wanyi language) meaning 'small'; *dou* is Greek for 'tooth'. The name alludes to the small molars found in species of this genus and to the fact that the posterior molars do not increase markedly in size from M2 to M4 as they appear to do in the otherwise similar *Neohelos tirarensis*.

Nimbadon lavarackorum n.sp. (Figs 2,3)

HOLOTYPE

The holotype is QMF23141, a left maxillary fragment containing M², M³ and the buccal half of P³.

ETYMOLOGY

The species is named after Sue and Jim Lavarack in recognition of their invaluable support in the field at Riversleigh and as founding members and hard working Councillors of the Riversleigh Society, a support group for Australian palaeontological research.

TYPE LOCALITY AND AGE

Henk's Hollow Locality (Archer & Flannery, 1987) occurs within the sequence of Tertiary limestones outcropping on Riversleigh Station, northwestern Queensland (Archer & Hand, 1984; Archer et al., 1989, 1991). It is stratigraphically near the top of the System C sequence as defined by Archer et al. (1989, 1991). This is interpreted to be stratigraphically higher than Site D (System A containing the Riversleigh Local Fauna;

Archer et al., 1991), Microsite (containing the Nooraleeba Local Fauna; Sigé, Hand & Archer, 1982; Hand, 1993) and Gag Site (near the base of System C, containing the Dwornamor Local Fauna; Flannery & Archer, 1984; Hand, 1985; Archer et al. 1991), but is close to (though still above) the level of Two Trees Site (containing the Two Trees Local Fauna Flannery & Archer, 1987). On the basis of its stratigraphic position and stage of evolution comparisons of its fossil mammals (work in preparation), the Henk's Hollow Local Fauna is tentatively interpreted here to be middle Miocene in age (Archer et al., 1989, 1991).

REFERRED SPECIMENS AND THEIR LOCALITIES

QMF23142 from the Henk's Hollow Locality, a left dentary containing P₃-M₅, is tentatively referred to this species, as are the following isolated teeth from Henk's Hollow: QMF23143, a right P³; QMF23144, a left P³; QMF23145, a left M²; QMF23146, a right M³; QMF23147, a left M⁴; QMF23148, a left ?M⁴; QMF23149, a right M⁴; QMF23150, a right M⁵; QMF23151, a right P₃; QMF23152, a left P₃; QMF23153, a right P₃; QMF23154, a left ?M₂; QMF23155, a right M₂, and QMF23160, a right M²⁻³, were collected from the Gag Site of the same plateau, Riversleigh Station.

REFERRED LOCALITIES AND AGES

The stratigraphic relationships of the Henk's Hollow Local Fauna and the Dwornamor Local Fauna are indicated above. At present, both are interpreted to be middle Miocene in age.

SPECIES DIAGNOSIS

This species is distinguished from *Nimbadon scottorum* n.sp. from Riversleigh's Fig Tree locality (see below) by its smaller size, relatively longer P¹, better developed hypocone on P³, less well-developed parastyle on M³ and probably more elongate posterior upper molars and less well developed postmetacrista but more discrete metastyle on M².

It is distinguished from the similar-sized *N. whitelawi* n.sp. by its almost square (rather than rectangular) upper molars.

DESCRIPTION

P³ is represented by three specimens: a LP³ from the holotype, QMF23141; an isolated RP³, QMF23143; and an isolated LP³, QMF23144. The tooth is widest across the protocone, sharply pinching in anteriorly and smoothly rounding posteriorly. It is subtriangular and is comprised

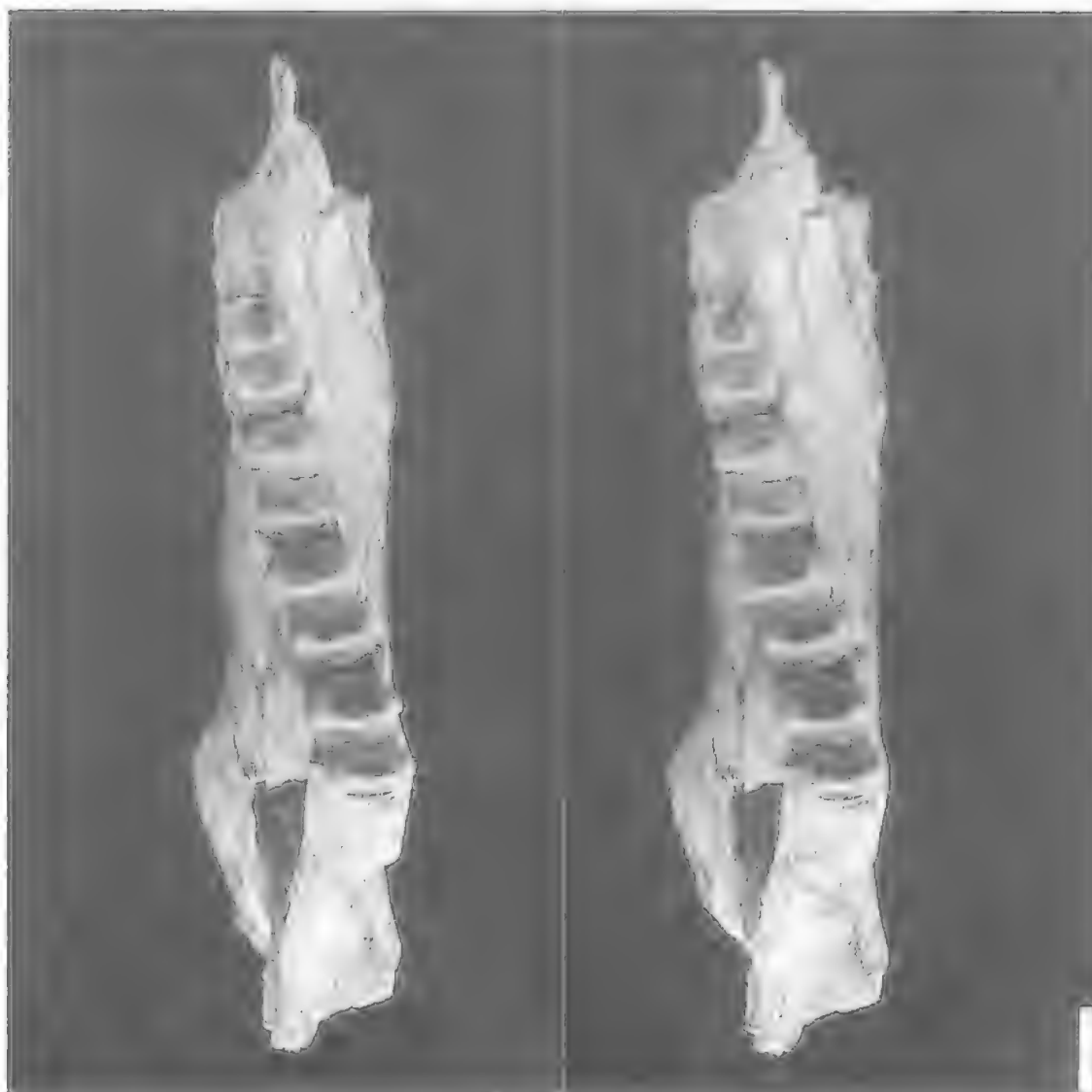


FIG. 3. *Nimbadon lavarackorum* n.gen., n.sp., Henk's Hollow Site, Riversleigh Station, QMF23142, left dentary with P₃, M₂, M₃, M₄ and M₅, occlusal stereopair. Bar indicates 10mm.

of four cusps: the parastyle, parametacone, protocone and hypocone (the latter however being variably developed). The parametacone is the highest cusp. It is blade-like with a strong shearing crest on the posterior edge and a short anterobuccally oriented apical crest. The protocone and parastyle are subequal in size. The hypocone is the smallest cusp and is even absent in one specimen (QMF23144). There is no suggestion of a division in the parametacone which is pyramid-shaped having relatively flattened anterior, buccal and lingual faces. The pro-

tocone is lingual to the parametacone and the hypocone lies posterobuccal to the protocone. The hypocone is more sharply separated by deep fissures from the buccal cusps than is the protocone. The parastyle is posteriorly inclined with a short anterolingually oriented apical blade. This large conical cusp forms a strong anterobuccal projection in the occlusal outline of the crown. It is separated from adjacent cusps by a chevron-shaped transverse cleft that is better-developed lingually than buccally. Posterior to this cleft, and on the anterior flank of the parametacone, a con-

spicuous ridge extends anterolingually from the tip of the parametacone to the anterolingual cingulum at a point anterobuccal to the base of the protocone. From the tip of the protocone, a poorly-defined transverse crest runs buccally until it almost meets (but does not) the parametacone ridge, its counterpart, at the commissure that separates the protocone and parametacone. Anterolingually, a very poorly developed (to ?absent) cingulum extends from the anterobuccal base of the protocone to the lingual base of the parastyle but does not continue up the flank of the parastyle. A cingulum is also developed posterobuccally from the buccal flank of the parametacone to the most posterior point of the crown (but is better-developed in some specimens than in others) and appears to be developed posterolingually from this point to at least the base of the hypocone. There is no evidence of an anterobuccal cingulum. From the tip of the parametacone, a prominent crest runs to the posterior margin of the tooth, dividing the posterolingual and posterobuccal cingula. A small crest runs posteriorly from the tip of the protocone to a swelling or cuspule. Another thin crest on the posterior face of the hypocone appears to converge with the posterolingual cingulum (at least in QMF23144). The tooth is two-rooted. The anterior root is conical and slightly anteriorly sloping; the larger posterior root is anteroposteriorly flattened and anteriorly convex. Many of the medial surfaces of the four crowns are covered in fine, poorly developed crenulations. There are two roots: one anterior oval one beneath the parastyle; and a much longer anteroposteriorly compressed root that extends transversely beneath the whole width of the posterior part of the crown.

M^2 . The first upper adult molar is known from the holotype, QMF23141, and ?an isolated left M^2 , QMF23145. It is a low-crowned almost square transversely lophodont tooth that is only slightly longer than wide. It is comprised of an anterior moiety, the protoloph, and a posterior moiety, the metaloph. Both are anteriorly convex. The paracone and metacone are similar in size as are the slightly shorter protocone and metaconule. The metaconule is slightly higher than the protocone and more lingually-situated. The metaloph is thus wider than the protoloph. The paracone and metacone are slightly closer together than are the protocone and metaconule. In the anterobuccal corner of the tooth a weak parastyle is developed at the buccal end of the short anterior cingulum. There is no metastyle although there is a prominent postmetacrista that extends from the

tip of the metacone to the posterior cingulum with which it merges. A weakly developed postparacrista on the posterior flank of the paracone extends toward the midvalley but stops short of contacting similar premetacristae that extend from the metacone and from just lingual to the metacone towards the midvalley. From the protocone and metaconule, wide but very faint crests extend posterobuccally across the posterior flanks of the protoloph and metaloph. From the protocone, this crest extends to the transverse valley near the midline; from the metaconule this crest extends to the posterior cingulum also near the midline of the tooth.

Wear facettes on these crests exhibit polish and parallel striations (particularly in QMF23145) suggesting that their function was maintained by thethesis against (respectively) the entoconid of M_2 and the metaconid of M_3 . The anterior cingulum extends from the parastyle around the lingual base of the protocone where it is interrupted and then continues across the lingual end of the transverse valley to the anterolingual base of the metaconule where it is interrupted and then continues around to the metastyle. There is no buccal cingulum. The M^2 may have been three-rooted with a cylindrical root beneath the paracone and another beneath the protocone and a single wide root beneath the metaloph. Precise thegotic facettes occur on the anterior trailing edges of the protoloph and metaloph blades. The anterior flanks of the protoloph and metaloph are "hollow-ground" in anticipation of the thegotic sharpening of the blades. Fine vertical crenulations on the flanks of the protoloph and metaloph produce secondary, vertical ?beta thegotic blades as the tooth sustains abrasive and thegotic wear.

M^{3-5} . M^{3-5} are similar to M^2 in basic morphology but are slightly larger and higher-crowned. The paracone is larger and more buccally-situated than the metacone. The protoloph and metaloph increase slightly in width from M^{2-4} . The parastyle and postmetacrista are markedly reduced in M^{3-5} such that in M^3 they are represented by terminal swellings in the anterior and posterior cingula respectively and are absent in M^4 and M^5 . In some specimens (e.g. M^3 in QMF23160), however, there is a very tiny cuspule on the posterior flank of the metacone of posterior molars. The postparacrista is less well-developed as are the crests from the protocone and metaconule. The mesostyle appears to be lacking. The part of the crown anterior to the protoloph is shorter and the swelling in the transverse valley better developed. The metaloph is much more strongly curved in

M³⁻⁵ and is more lingually offset with respect to the protoloph.

Dentary. QMF23142, a dentary containing P₃, M₂ 5, is tentatively referred to this species. It is of a size appropriate for some of the referred upper molars of this species and in its suite of plesiomorphic zygomaturine features (e.g. its lack of a posteriorly increasing molar size gradient), is analogous to the phylogenetic state of the upper molars of *N. lavarackorum*. However, because the specimen appears to be approximately 10% larger than the holotype, there is still some slight doubt about the propriety of referring this dentary to *N. lavarackorum*.

The dentary is badly fractured and is missing the incisor, medial symphysis, angle and ascending ramus. It is deepest below the hypolophid of M₄. The ventral border slopes posteriorly upward from this point and anteriorly upward to at least the hypolophid of M₂. The anterior edge of the coronoid process leads posterodorsally from the body of the horizontal ramus. The postalveolar process is missing. There is no distinct digastric fossa and the area beneath the leading edge of the coronoid process is smooth suggesting that the masseteric fossa was not deep. The mental foramen is located approximately 4mm in front of a vertical line marking the most anterior edge of the P³ crown. It is round in lateral view and opens anterodorsally onto the buccal surface of the diastemal region. Although the mandibular foramen is not preserved, the mandibular canal is represented by a sulcus at about the level of the tooth row.

The P₃ is preserved in QMF23142 as well as QMF23152, an isolated LP₃, QMF23153, an isolated RP₃ and QMF23151, an isolated RP₃. The tooth is longer than it is wide and more narrow anteriorly than posteriorly. It bears a central principal cusp, the protoconid, and a much smaller medially positioned posterior cingular cusp. These are joined by a prominent longitudinal shearing crest that also extends anteriorly from the protoconid to terminate as a cuspule or cingular swelling at the anterior edge of the crown. Lingual to the principle central cusp there is a variably distinguished cuspule (stylid or vertical cristid). This structure is the apex of a vertical flanking crest that extends ventrally to a point just posterior to the lingual base of the protoconid. This crest is most conspicuous in posterior view. A posterolingual cingulum leads posteriorly from the base of this crest to the base of the posterior cusp. A similar but much less well-developed vertical cristid extends ventrally from the buccal

apex of the protoconid. Taken together, these flanking cuspules and their associated vertical cristids comprise a transverse structure that intersects the crown at its apex at right angles to the main longitudinal shearing cristid. The posterior cingulum is much better developed than the anterior cingulum which is present only at the anterolingual tip of the crown. The posterior cingulum extends from the lingual base of the protoconid to the posterior cusp where it is met by the buccal base of the protoconid but is best developed in the region of the posterior cusp where it is met by the main longitudinal crest of the crown. In this area of intersection, the posterior cingulum is conspicuously crenulated in some specimens (i.e. QMF23152 and QMF23153) and slightly less so in others (i.e. QMF23151). In QMF23152, a wear facette on the posterobuccal cingulum, possibly produced by the P³ parametacone, is developed which is not seen in other specimens. In this same specimen, just anterior to the crenulated posterior cingulum, a transverse crest extends anterolingually from the tip of the posterior cusp to the posterolingual cingulum. In all specimens, a wear facette for M₂ is developed at the tallest point of the posterior cingulum. The tooth is double-rooted, the anterior root being conical in shape, the posterior root being anteroposteriorly flattened.

Specimens QMF23152 and QMF23153, although similar in morphology, are considerably smaller than the P₃ preserved in the dentary. The P₁ in this species might be sexually dimorphic.

M₂. The M₂, known from QMF23142 and QMF23154? (and the Gag Site QMF23155), is an elongate, subrectangular tooth that is narrower anteriorly than posteriorly. The trigonid of M₂ is represented by a transverse protolophid and an arcuate anterolingually directed paracristid that extends to the anterior margin of the tooth. From the protoconid a short indistinct crest (?protocristid) appears to extend posterobuccally to terminate in a slight swelling which is perhaps the protostylid. From the metaconid, a crest extends anteriorly a short distance. From the entoconid, a short entocristid extends anterolingually.

In occlusal view, the paracristid is convex buccally, the protolophid is transverse or very slightly posteriorly convex and the hypolophid is markedly posteriorly convex. The protolophid is narrower than the hypolophid. An anterior cingulum is present both buccal and lingual to the anterior end of the paracristid. The cingulum on the buccal side is not preserved in QMF23142, is distinct (between the protolophid and hypolo-

phid) in QMF23155 but not in QMF23154. There is no lingual cingulum or cristid obliqua in QMF23142 but there is a lingual cingulum in QMF23155 (again between the protolophid and hypolophid). The posterior cingulum connects the posterior base of the hypoconid to that of the entoconid. A wear facette is developed at the midpoint of the posterior cingulum. Distinct wear facettes extend along the posterior lengths of the protolophid and hypolophid. In lingual view, the floor of the transverse valley is U-shaped. The protoconid is taller than the subequal metaconid, hypoconid and entoconid. The tooth is double-rooted but these are not well preserved in the isolated teeth QMF23154 and QMF23155.

QMF23154 ($M_2?$) has a paracristid and premetacristid that are much less distinct than those preserved in the dentary and Gag Site specimen. Only the paracristid extends to the anterior cingulum of the tooth. In this specimen, the enamel on the posterior face of the protolophid has prominent vertical crenulations. The cristid obliqua is also distinct although low and extends as a minor vertical crenulation on to the posterior flank of the protolophid.

M_{3-5} . Unlike M_2 , trigonids of the posterior molars lack a prominent paracristid and are more rectangular in appearance with the protolophid being slightly wider than the hypolophid in M_{3-5} .

In M_3 , the protolophid and hypolophid are approximately the same width. The paracristid forms a poorly-defined vertical crest that extends only partly down the anterior face of the protolophid. The premetacristid is also poorly defined and extends approximately the same distance. Protolophids and hypolophids become more posteriorly convex from M_2 to M_5 . In M_{4-5} , the protolophids are markedly wider and the hypolophids are lingually displaced. M_4 and M_5 are larger than M_3 .

Nimbadon whitelawi n.sp.
(Fig. 4)

HOLOTYPE

The holotype and only known specimen is NMVP186506. It preserves the palate, RP^3-M^3 and LP^3-M^3 . All teeth except LP^3 are damaged and LM^3 and RM^3 are missing parts of their posterior halves.

ETYMOLOGY

This species is named after Michael Whitelaw who assisted in the collection and processing of specimens from Bullock Creek.

TYPE LOCALITY AND AGE

The type locality is fossil vertebrate locality WV 113 in Bultitude (1973) ($17^\circ 7'S$, $131^\circ 32'E$), the Horseshoe West locality of the Camfield Beds at Bullock Creek, Camfield Station, northwestern Northern Territory. The Bullock Creek Local Fauna (Plane & Gatehouse, 1968; Archer & Bartholomai, 1978; Rich et al., 1991; Archer & Hand, 1984; Murray & Megirian, 1990, 1992) is currently interpreted to be ?middle Miocene, i.e. immediately post-Wipajiri, in age (Woodburne et al., 1985; Murray, 1990a; Murray & Megirian, 1990, 1992).

SPECIES DIAGNOSIS

This species is distinguished from *N. lavarackorum* and *N. scottorum* by its markedly more elongate (i.e. less square) upper molars and relatively more anteriorly situated buccal swelling on P^3 . It is also distinguished from *N. scottorum* by its relatively much longer P^3 and markedly convex anterior and posterior molar crown margins such that these teeth have a much reduced area of interdental contact.

DESCRIPTION

The species is described insofar as it differs from *Nimbadon lavarackorum*.

The palate preserves most of the right and a large part of the left maxillae and small fragments of the left and right palatines. Anteroventrally, the palate is fractured at or behind the premaxillo-maxillary suture. Posteroventrally, it preserves the maxillo-palatine suture. The latter extends anteriorly to a point medial to the posterior part of M^1 . Palatal ridges extend longitudinally and anteriorly along the length of the palate from the level of M^1 . The right diastemal crest runs antero-lingually. The tooth rows are parallel to slightly convex buccally. Anteriorly, doming of the median region of the palate is marked. It extends posteriorly to the level of the rear of M^2 and, though shallowing perhaps, anteriorly to at least just behind the premaxillo-maxillary boundary. There is a pair of nutrient foramina on the right side of the palate medial to P^3 and on the left side a single foramen. Medial to the hypoloph of M^2 , is another tiny foramen on each side of the palate. The infraorbital foramen canal is about 10mm in length. The infraorbital canal opens onto the face 14mm above the anterior edge of the P^3 alveolus. Sutural relationships of the palatine, lacrimal, jugal and maxillary bones are unclear. There is no evidence for maxillary or palatal vacuities although the anterior and posterior ex-

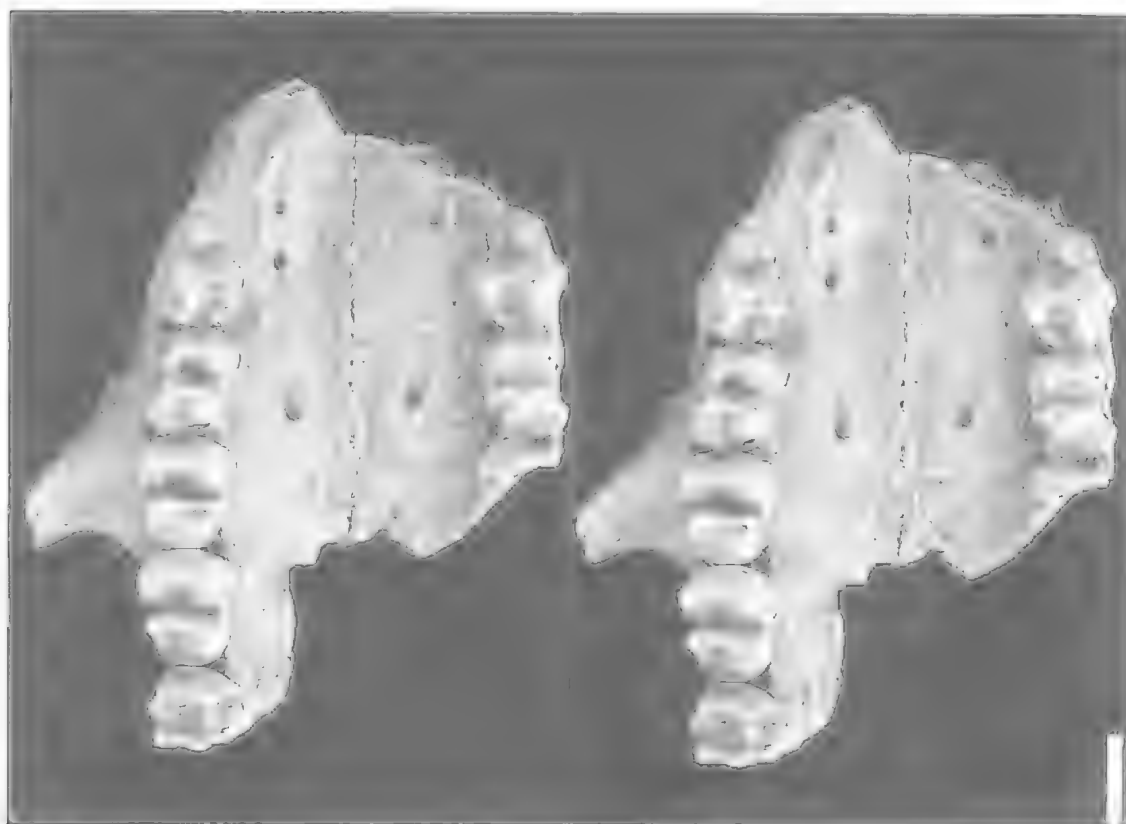


FIG. 4. *Nimbadon whitelawi* n.sp., Bullock Creek, Northern Territory, NMVP186506, palate with RP^3 - M^5 and LP^3 - M^3 , occlusal stereopair. Bar indicates 10mm

tremities of the palate are missing. The maxillary process near the roof of the zygomatic arch, although damaged, is down-turned and conspicuous but does not extend ventrally below the level of the palate. There appears to have been a very reduced orbital wing of the maxilla, although bone boundaries in this region are unclear.

Upper dentition. The P^3 differs from most specimens (all except QMF23144 AR5513) of *N. lavarackorum* in the greater degree of development of the hypocone. In *N. whitelawi* the parastyle appears to be less posteriorly inclined and the anterolingually-directed crest that extends from the parametacone to the anterolingual cingulum is less distinct although it is possibly diminished by wear. It nevertheless approaches the buccal crest from the protocone at a steep angle rather than perpendicular.

The M^2 on both sides of the holotype is damaged buccally and lingually. However, it appears to differ from both Riversleigh species of *Nim-*

badon in being longer relative to P^3 and in appearing to be rectangular rather than square.

The M^3 appears to differ from the Riversleigh species in a similar way as M^2 , but it appears to be relatively even more elongate. M^2 and M^3 are approximately equal in length.

The M^4 differs less from that tooth in the other species of *Nimbadon*.

All of the cheekteeth of *N. whitelawi* appear to differ from those of *N. scottorrorum* in having anteriorly and posteriorly markedly convex tooth margins so that the crowns abut with limited contact.

Nimbadon scottorrorum n.sp. (Fig. 5)

HOLOTYPE

The holotype and only known specimen is QMF23157 (formerly SAMP27815), a right maxillary fragment containing P^3 , M^2 , M^3 , M^4 and M^5 . While P^3 and M^2

are intact, M^{3-5} are missing the buccal margins of the crown.

ETYMOLOGY

The species is named after Sue and Don Scott-Orr, in recognition of their long-term support for the Riversleigh Palaeontological Research Project. With the Lavaracks, they are also founding members and Councillors of the Riversleigh Society.

TYPE LOCALITY AND AGE

The type locality, Fig Tree Site, is adjacent to Godthelp Hill, Riversleigh Station, northwestern Queensland. It is laterally adjacent to units regarded by Archer et al. (1989, 1991) to be part of System B although it may actually be from the basal part of System B or even upper part of System A, hence stratigraphically below Henk's Hollow (upper part of System C; Archer, Hand & Godthelp, 1986) and Gag Site (lower part of System C; Flannery & Archer, 1984; Hand, 1985) and possibly above or equivalent to Microsite (?System A; Sigé, Hand & Archer, 1982; Archer et al., 1989, 1991) and Site D (System A; Tedford, 1967; Archer et al., 1989, 1991). On this basis and stage of evolution comparisons of the marsupials in these faunas, the Fig Tree Local Fauna is interpreted to be ?late Oligocene-early Miocene in age.

SPECIES DIAGNOSIS

This species is distinguished from *Nimbadon lavarackorum* and *N. whitelawi* by its larger size, anteroposteriorly compressed P^3 (which is much shorter than any upper molar), its more robust cingula on all cheekteeth and its greater parastylar development in M^{2-3} (contributing to the squared appearance of these teeth). It also has less convex anterior and posterior molar crown margins which therefore have much wider interdental contact with each other.

It is further distinguished from most (but not all) *N. lavarackorum* by its much smaller hypcone on P^3 .

DESCRIPTION

Nimbadon scottorum differs from *N. lavarackorum* and *N. whitelawi* as follows:

The P^3 is markedly anteroposteriorly compressed such that it is almost as wide as it is long

and is subrounded in shape. Unlike *N. lavarackorum*, in which P^3 is equal in length or longer than any adult upper molar, in *N. scottorum* this tooth is the shortest in the tooth row. The hypcone appears to have been very poorly developed.

The anterobuccal corner of M^2 has a much squarer appearance due to greater parastylar development in the anterior cingulum. This is true also of the posterobuccal corner of the tooth where metastylar development occurs mid-way along the postmetacrista.

Parastylar development in M^3 is relatively marked compared with its condition in *N. lavarackorum*. The teeth are buccally fractured in M^{3-5} making it impossible to determine the degree of development of the buccal cusps in M^{4-5} .

DISCUSSION

The three diprotodontids described here appear to comprise a new clade of zygomaturines. As species of the new genus *Nimbadon*¹, they may be distinguished from other zygomaturines by, among other features, a combination of upper premolar attributes. Premolar morphology was extensively used by Stirton (1967) and Stirton et al. (1967) to help resolve distinctions between diprotodontid lineages and has subsequently been used by most workers. Few other character systems have been found to be as useful in distinguishing probable inter-relationships among Tertiary diprotodontids.

Since Stirton et al.'s (1967) review of Tertiary diprotodontids, diverse diprotodontoid materials have been collected from Oligo-Miocene fossil sites at Riversleigh, Bullock Creek, Alcoota and Beaumaris and from Pleistocene sites in New Guinea (e.g. Flannery, 1992) and many areas of Australia. This material includes specimens representing new genera and probably new diprotodontoid subfamilies. Murray (1986, 1990a,b) has named several new Tertiary taxa but the bulk of the material, particularly from Riversleigh sites, is yet to be described. As a result of the new discoveries, the superfamily Diprotodontoidae is in need of major revision.

At present (e.g. the reviews of Archer, 1984; Aplin & Archer, 1987; Marshall, Case & Woodburne, 1989; Murray, 1990b) two diprotodontoid families are recognised: the Palorchestidae and the Diprotodontidae with two subfamilies, the

¹ The generic name *Nimbadon* was used by Murray (1990b) in a cladogram of hypothetical phylogenetic inter-relationships among Miocene diprotodontids. However Murray did not designate a species of *Nimbadon* in the cladogram or in the ensuing discussion, and, as outlined in Article 13B of the Code of Zoological Nomenclature, '*Nimbadon*' was thus used as a *nomem nudum*.

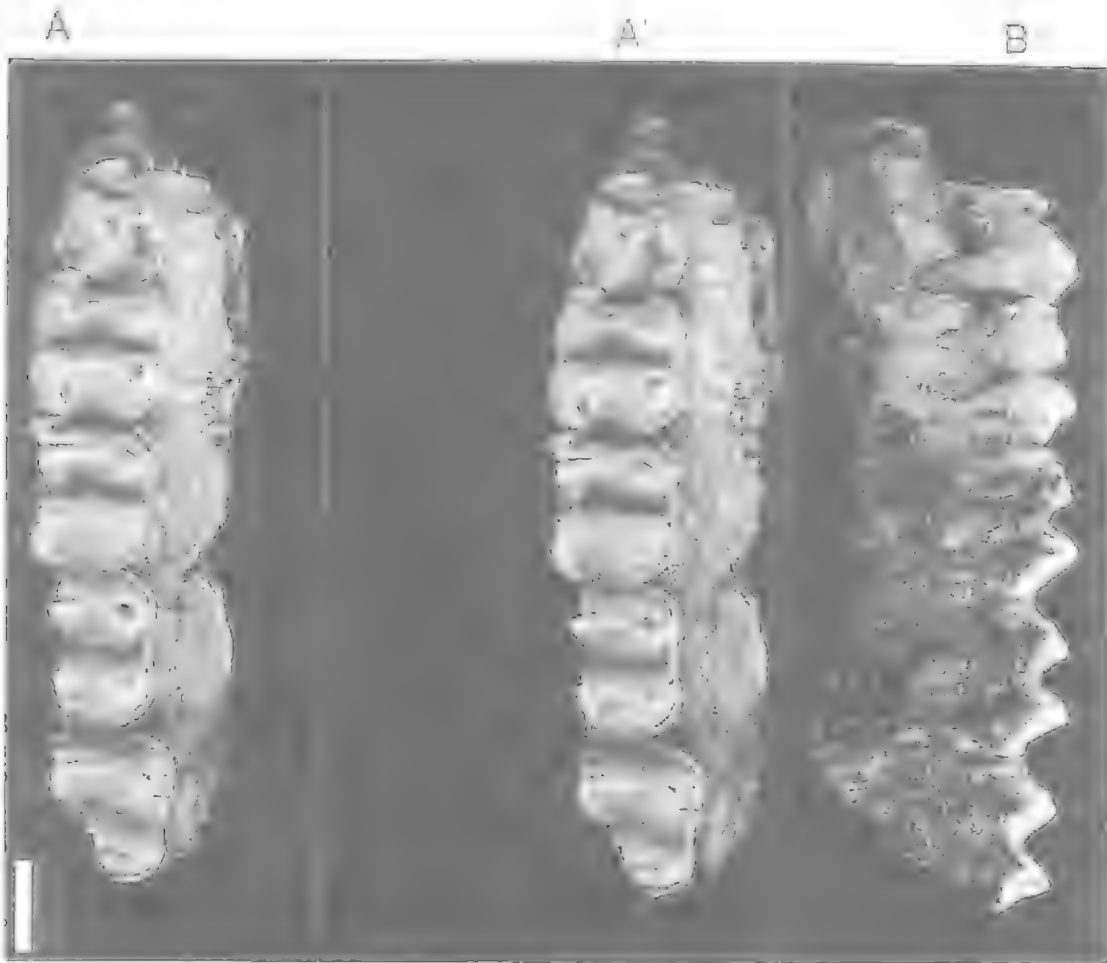


FIG. 5. *Nimbodon scottorum* n.sp., Fig Tree Site, Riversleigh Station, QMF23157, right maxillary fragment with RP^2-M^2 , A-A', occlusal stereopair; B, buccal view. Bar indicates 10mm.

Diprotodontinae and the Zygomaturinae. Although zygomaturines have traditionally (e.g. Stirton et al., 1967) been considered to be among the most primitive of diprotodontoids, it is by no means certain that this is so (Murray, 1990b). It is not clear what might be used as an appropriate outgroup in a phylogenetic analysis of zygomaturines nor, consequently, are polarities of character state morphoclines within the Zygomaturinae confidently determined.

Murray (1990b) has discussed other difficulties in analysing diprotodontid phylogenetics. He notes that despite the fact that many Tertiary diprotodontids are represented by almost-complete skull and dentary material, discontinuities in some character complexes and the continuously varying nature of others tend to obfuscate clarification of relationships between taxa. Con-

siderable variability in cranial morphology has been observed in some zygomaturines (e.g. in a *Neohelos* sample from the Bullock Creek Local Fauna; P. Murray, pers.comm.), and the molar dentitions of the zygomaturines *Plaisiodon centralis* Woodburne, 1967 and *Alkwertatherium webbi* Murray, 1990b and the diprotodontine *Pyramios alcootense* Woodburne, 1967 have been found to overlap in size and morphology (Murray, 1990b).

It is perhaps a measure of the difficulties encountered in determining species and generic boundaries for diprotodontids that *Nimbodon* is one of few non-monotypic Tertiary zygomaturine genera, the others being *Kolopsis* Woodburne, 1967 and *Zygomaturus* Owen, 1859.

Recognition of the genus *Nimbodon* has been facilitated by re-diagnosis of *Neohelos* Stirton,

1967 based on new material obtained by Archer and colleagues 20 years after the original material was collected by Stirton and colleagues from the Leaf Locality of Lake Ngapakaldi, South Australia. This provides novel information about the anterior morphology of P^3 , which exhibits, among other distinctive features, a large, erect parastyle. This feature is also present in specimens referred to *Neohelos* from the Bullock Creek and Riversleigh Tertiary faunal assemblages (Plane & Gatchouse, 1968; Plane, 1971; Rich et al., 1982; Murray & Megirian, 1990, 1992; Archer et al., 1989, 1991).

In his review of Oligo-Miocene diprotodontid taxa, Murray (1990b) postulates a number of phylogenetic hypotheses, only one of which is expressed in his cladogram (fig. 14). The latter is based primarily on analysis of dental characters (in particular, P^3), using species of the Oligo-Miocene palorchestid genera *Ngapakaldia* and *Pitikantia* as outgroups. In it, Murray identifies species of *Kolopsis* and *Zygomaturus* as the most derived diprotodontids and *Neohelos tirarensis* as their closest relative. Species of *Nimbadon* form the sister-group to the *Neohelos-Kolopsis-Zygomaturus* clade, with *Plaisiodon centralis* being the sister-group of a *Nimbadon-Neohelos-Kolopsis-Zygomaturus* clade, *Kolopsoides cultridens* Plane, 1967 the sister-group of a *Plaisiodon-Nimbadon-Neohelos-Kolopsis-Zygomaturus* clade and *Alkwertatherium webbi* the most plesiomorphic of zygomaturines. Species of *Pyramios*, *Euryzygoma*, *Bematherium* and *Diprotodon* form a separate (diprotodontine) clade. *Raemveoltherium yutkolai* Rich, Archer & Tedford, 1978 from the Late Oligocene Namba Formation of Lake Pinpa, South Australia, is interpreted to be the most plesiomorphic member of the family Diprotodontidae.

On the basis of his broader study of dental and cranial characters, however, Murray (ibid.) concludes that there are probably two minor zygomaturine lineages: one represented by species of *Nimbadon*, *Neohelos* and *Kolopsis*, a group he suspects may consist of taxa related largely by symplesiomorphies; the other lineage possibly containing species of *Alkwertatherium*, *Plaisiodon* and *Kolopsoides*, although for this clade he can find even less concrete evidence. He suggests that these two lineages might be related through common ancestry in *Nimbadon*. He also suggests in the text, but not the cladogram, that *Nimbadon* species could represent basal zygomaturines with some specific affinity to *Plaisiodon centralis* and *Neohelos tirarensis*, and that *Plaisiodon centralis*

is more closely related to *Alkwertatherium webbi* than to any other zygomaturine.

A phylogenetic hypothesis of diprotodontid inter-relationships, including the three new *Nimbadon* species and broadly based on Murray's cladistic analysis of dental characters, is given in Fig. 6. The polarity of some characters has been interpreted differently from Murray (1990b) but basic intergeneric relationships remain unchanged except for the position of *Plaisiodon centralis*.

In Fig. 6 and Murray (1990b), the Zygomaturinae are clustered on the basis of a large parastyle on P^3 which is separated from the parametacone by a deep cleft. The *Kolopsoides-Plaisiodon-Nimbadon-Neohelos-Kolopsis-Zygomaturus* clade shares as a synapomorphy development of a hypocone in P^3 . The basic proportions of P^3 are apomorphically shared by species of the *Nimbadon*, *Plaisiodon*, *Neohelos* and *Kolopsis* clade (but see Murray, 1990b), with a division in the parametacone interpreted to have occurred subsequently in the *Kolopsis* lineage. Retraction of the mesostyle towards the cingulum in P^3 clusters species of *Neohelos* and *Kolopsis* (Murray, 1990b).

In both cladograms, the posteriorly inclined (or hooked) parastyle of P^3 in species of *Nimbadon* is regarded to be apomorphic. Only one other zygomaturine exhibits this feature — *Plaisiodon centralis*. Although species of *Nimbadon* are readily distinguished from *P. centralis* by aspects of upper premolar morphology (including in *P. centralis* the very large hypocone and the lingual crest from the parametacone linking to the protocone rather than the anterolingual cingulum) as well as by their small size, lack of a posteriorly increasing molar gradient and absence of metalophs on lower molars, sharing of the distinctively shaped parastyle may indicate an albeit distant phylogenetic relationship.

Although the three taxa described here as species of *Nimbadon* may, when better known, prove not to be monophyletic, all exhibit the distinctive crest on P^3 running lingually from the parametacone to the protocone then anteriorly to the anterolingual cingulum, a feature not previously noted in any other diprotodontoid taxa. Other features that characterise the new taxa include their small size and an $M_2:M_1$ length ratio which approaches 1.0. The latter are interpreted here and generally (see below) to be plesiomorphic features among diprotodontids, but they might equally be interpreted to represent apomorphic reversals within certain zygomaturine lineages.

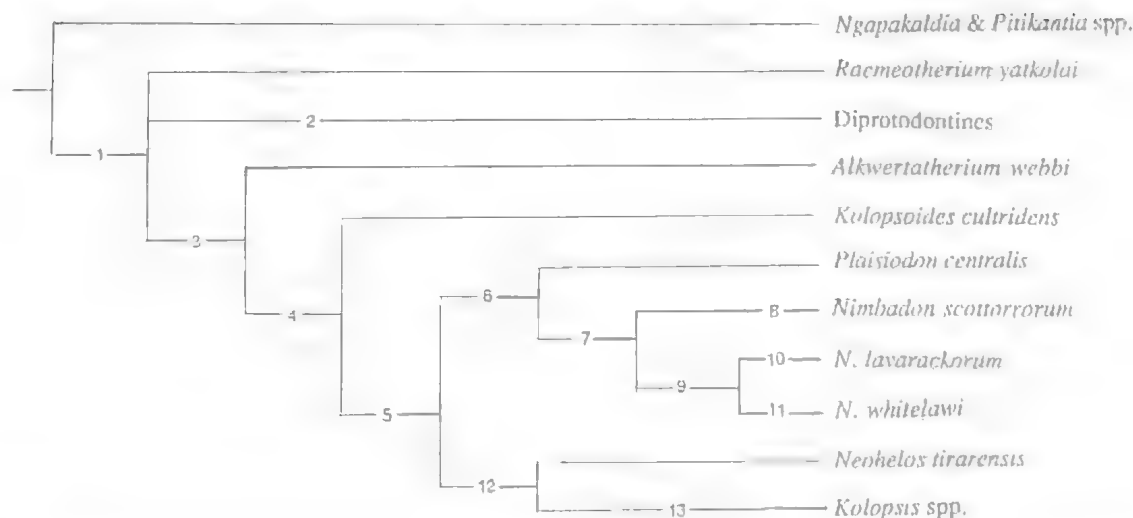


FIG. 6. A phylogenetic hypothesis of zygomaturines, broadly based on Murray's (1990b) cladistic analysis of dental characters in the Diprotodontidae. Apomorphies are as follows: 1, loss, incorporation or suppression of styler cusps C and D with respect to the lophi on upper molars; 2, reduction of paralophid crest on M_2 ; 3, large parastyle on P^1 separated from parametacene by a deep cleft; 4, development of a hypocone on P^1 ; 5, basic proportional similarity of P^2 ; 6, hooked parastyle on P^2 ; 7, apical blade and diagonal crest on P^2 ; 8, shortening of P^3 ; 9, elongation of posterior molars (i.e. at least $M3-4$); 10, hypertrophy of P^1 hypocone; 11, elongation of anterior molars, i.e. $M2$; 12, mesostyle on P^3 retracted towards cingulum; 13, division in P^3 parametacene.

We can, however, find no pressing evidence to closely align individual species of *Nimbadon* with any previously known zygomaturine taxa.

Most zygomaturines — including species of *Zygomaturus*, *Kolopsis*, *Kolopsoides* and *Plaisiodon* — exhibit a marked increase in molar size from $M2$ to $M4$ (with an $M2-M4$ length ratio of 0.85 or less) with $M5$ generally decreasing in size (see also Rich, Archer & Tedford, 1978). Whether this is also true of topotypical *Neohelos tirarensis* is not known but *Neohelos* specimens from Bullock Creek and most from Riversleigh exhibit this feature.

A molar gradient of $M2:M4$ length approaching 1.0 is regarded by Rich, Archer & Tedford (1978) to be plesiomorphic in zygomaturines. *Raemotherium yatkolai*, commonly considered to be the most primitive of known zygomaturines (but see Murray, 1990b, and below) and represented by a dentary, isolated lower teeth and an upper incisor from the Oligo-Miocene Namba Formation of Lake Pinpa, also has uniformly sized molars (with a ratio of $M2:M4$ length of 0.96). Palorchestids and diprotodontines variably exhibit this feature and one of the oldest known diprotodontoids, represented in the early Miocene Geilston Bay Local Fauna by a maxilla preserving part of M^2 and M^3 , also has uniformly sized molars. The latter is similar in size to *R.*

yatkolai but is tentatively considered by Tedford et al. (1975) to be a palorchestid. Apart from its slightly larger size, *Nimbadon lavarackorum*, the only species of the genus so far represented by lower molars, like all other zygomaturines differs from *R. yatkolai* in its reduction of anterior entocristids. *Nimbadon* species further differ from *Raemotherium yatkolai* in being larger; in having a more massive dentary which, in transverse width, is approximately twice the width of $M3$; in having less well developed cristids obliqua; relatively wider trigonids on all molars; trigonid of $M2$ nearly the same width as the talonid (in contrast to *R. yatkolai* where it is markedly narrower); metaconid of $M2$ as high as the protoconid and associated with a prominent, steeply inclined, swollen anterior buttress; metacristid of $M2$ transversely oriented (in contrast to *R. yatkolai* where it is posterobuccally oriented); "arcuate" (rather than anteroposteriorly rectilinear) paracristid on $M2$; and lophids of lower molars less occlusally concave.

It is possible that molar size gradients in zygomaturines are allometrically related to body-size, with larger animals exhibiting relatively larger posterior molars. From Oligo-Miocene deposits on Riversleigh Station, small diprotodontines have been found with $M2:M4$ length gradients approaching 1.0. Equally, however, the

larger of the Riversleigh species of *Nimbadon* described here (*N. scottorum*) appears to have been similar in overall size to at least one undescribed Riversleigh *Neohelos* that shows a marked progressive increase in molar size from M2 to M4. It seems, therefore, that the feature is not always dependent on absolute size although it may vary allometrically within lineages. In Fig. 6 it has been interpreted to be autapomorphic within various clades.

Intragenetic relationships within *Nimbadon* are not much easier to interpret. *Nimbadon whitelawi* differs from both *N. lavarackorum* and *N. scottorum* in its markedly more elongate upper molars (particularly with respect to *N. scottorum*) and relatively more anteriorly situated buccal swelling on P³. *Nimbadon lavarackorum* differs from *N. scottorum* in its smaller size, less well-developed parastyle on M³ and probably more elongate posterior upper molars and less well developed postmetacrista but more discrete metastyle on M². *Nimbadon scottorum* is larger than both *N. lavarackorum* and *N. whitelawi*, has more robust cingula on all cheek-teeth and greater parastylar development in M²⁻³ (contributing to the squared appearance of these teeth). Within *Nimbadon*, features such as the hypertrophy of the P³ hypocone in some specimens of *N. lavarackorum* and the shortening of P³ in *N. scottorum* appear to be autapomorphic features unique to those species. The most striking differences between the taxa lie in the degree of squaring (or conversely elongation) of the upper molars.

There are two quite different phylogenetic interpretations of *Nimbadon* species, depending on whether elongation (versus squaring) of the upper molars is considered to be plesiomorphic or apomorphic. Commonality would indicate squared upper molars to be plesiomorphic among diprotodontian marsupials including phalangerids, vombatiforms and even plesiomorphic kangaroos. However, within the Diprotodontidae the otherwise 'plesiomorphic' (i.e. simple) *Rae-mootherium yatkolai* has relatively elongate lower molars and, although no uppers molars are yet known, they too would probably have been relatively elongate, using as a guide the relative proportions of the upper and lower molars of *N. lavarackorum*. It should be noted that the presumption that *R. yatkolai* is the most plesiomorphic diprotodontid is based on its simplicity. Simplicity, however, often characterises the smaller members of some diprotodontian lineages (e.g. pseudocheirids and macropodids) and

all members of other lineages with ubiquitously small members (e.g. burramyids and acrobatids).

Because so few dental character systems have been found to be useful in diprotodontid systematics, polarity swings of this kind greatly influence the interpreted relationships of taxa and their biostratigraphic significance. If elongation is plesiomorphic among diprotodontids, then *N. whitelawi* would be the most plesiomorphic of the three *Nimbadon* species. Its presence in the middle Miocene Bullock Creek Local Fauna and the presence of what would then be interpreted to be the most apomorphic in the older Fig Tree Local Fauna, would not be support for the currently understood stratigraphic relationships. If, on the other hand, elongation is interpreted to be apomorphic, then the most derived species (*N. whitelawi*) occurs in one of the younger faunas and the most plesiomorphic (*N. scottorum*) in the oldest of the faunas (Fig Tree).

The stratigraphic relationships of the fossil assemblages have been discussed in the Systematics section above. The Fig Tree Site occurs adjacent to units regarded to be part of Riversleigh's System B sequence as defined by Archer et al. (1989, 1991), though it may actually be basal System B or upper System A, and is interpreted to be late Oligocene to early Miocene in age. The Henk's Hollow Site occurs near the top of Riversleigh's System C sequence and the Gag Site near its base. Both lie stratigraphically above the Fig Tree level. On the basis of their positions and stage of evolution comparisons of their fossil mammals, they are interpreted to be middle Miocene in age and are probably similar in age to the Bullock Creek assemblage. The Bullock Creek Local Fauna has been interpreted by Woodburne et al. (1985), Murray (1990a) and Murray & Megirian (1990) to be middle Miocene, i.e. immediately post-Wipajiri, in age.

On balance, we consider the phylogenetic relationships of *Nimbadon* species (Fig. 6) to approximately correspond to current understanding of the relative ages of the deposits from which the specimens were obtained but conclude that for the moment at least caution is appropriate in attempts to use zygomaturines to correlate northern Australian Tertiary mammal-bearing faunas.

ACKNOWLEDGEMENTS

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Australian Museum enabled N. Pledge to collect and prepare the holotype of *N. scottorum*. Work at Riversleigh has been supported by the Australian Research Council, the Department of the Arts, Sport, the Environment and Territories, National Estate Programme Grants (Queensland), the Australian Geographic Society, ICI, the Queensland Museum and the University of New South Wales. During the course of this work, S. Hand and H. Godthelp were supported by a University of New South special research grant. The authors thank Dr Peter Murray for his constructive criticism of the manuscript, and Dr David Ride who provided helpful nomenclatural advice. The photos were taken by Ross Arnett of the University of New South Wales.

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DESCRIPTION OF A NEW SPECIES OF *CHAMA* FROM THE GULF OF
CARPENTARIA WITH COMMENTS ON *PSEUDOCHAMA* ODHNER (MOLLUSCA:
BIVALVIA: CHAMIDAE)

JOHN M. HEALY, KEVIN L. LAMPRELL AND JOHN STANISIC

Healy, J.M., Lamprell, K.L. & Stanisic, J. 1993 06 30: Description of a new species of *Chama* from the Gulf of Carpentaria with comments on *Pseudochama* Odhner (Mollusca: Bivalvia: Chamidae). *Memoirs of the Queensland Museum* 33(1): 211-216. Brisbane. ISSN 079-8835.

A new species of Chamidae, *Chama isaacooki* sp.nov., is described from northern Australia and a key to the Australian Chamidae presented. In addition, the phenomenon of left versus right valve attachment in chamids is discussed, particularly in relation to recognition of the genus *Pseudochama* Odhner, 1917. It is concluded that the identity of valve attachment is not a reliable, sole basis for distinguishing *Pseudochama* from *Chama*. □ *Mollusca, Bivalvia, Chamidae, new species, taxonomy, Pseudochama.*

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The Chamidae (Superfamily Chamoidea) is a widespread and common family of (typically) attached heterodont bivalves, characterized by pronounced leaf-like or spinose ornamentation, coiled umbones and often marked disparity in valve size. The living chamids of Australia have most recently been treated by Lamprell & Whitehead (1992), but the family has yet to be formally revised. During our recent investigations we have had the opportunity to examine numerous specimens from the various Australian State museums as well as material from a number of large private collections. This work revealed the existence of many synonyms as well as a new species from the Arafura Sea and the Gulf of Carpentaria. In the present paper we describe this species of *Chama* and compare it to other chamids from the Indo-Pacific region. We also take the opportunity to discuss Odhner's (1917) claim that *Pseudochama* Odhner can be separated from *Chama* solely on the basis of the valve of attachment (left versus right valve).

Abbreviations used in text: AM = Australian Museum; QM = Queensland Museum; WAM = Western Australian Museum; MV = Museum of Victoria; Q = Queensland; lv = left valve; rv = right valve; pv = paired valves; L = length; H = height; W = width..

MATERIAL AND METHODS

This study is based primarily on material held in the Australian Museum (Sydney), Museum of Victoria and Queensland Museum as well as numerous specimens in private collections includ-

ing the Lamprell collection. All measurements were made with Vernier callipers.

SYSTEMATICS

Superfamily CHAMOIDEA Lamarck, 1809
Family CHAMIDAE Lamarck, 1809
Chama Linnaeus, 1758

Type species: *Chama lazarus* Linnaeus, 1758; SD Children, 1823

Chama isaacooki sp.nov.
(Figs 1-4, Table 1)

ETYMOLOGY

The name honours the memory of Isaac Cook, son of Mr Steve Cook who provided the material for this study.

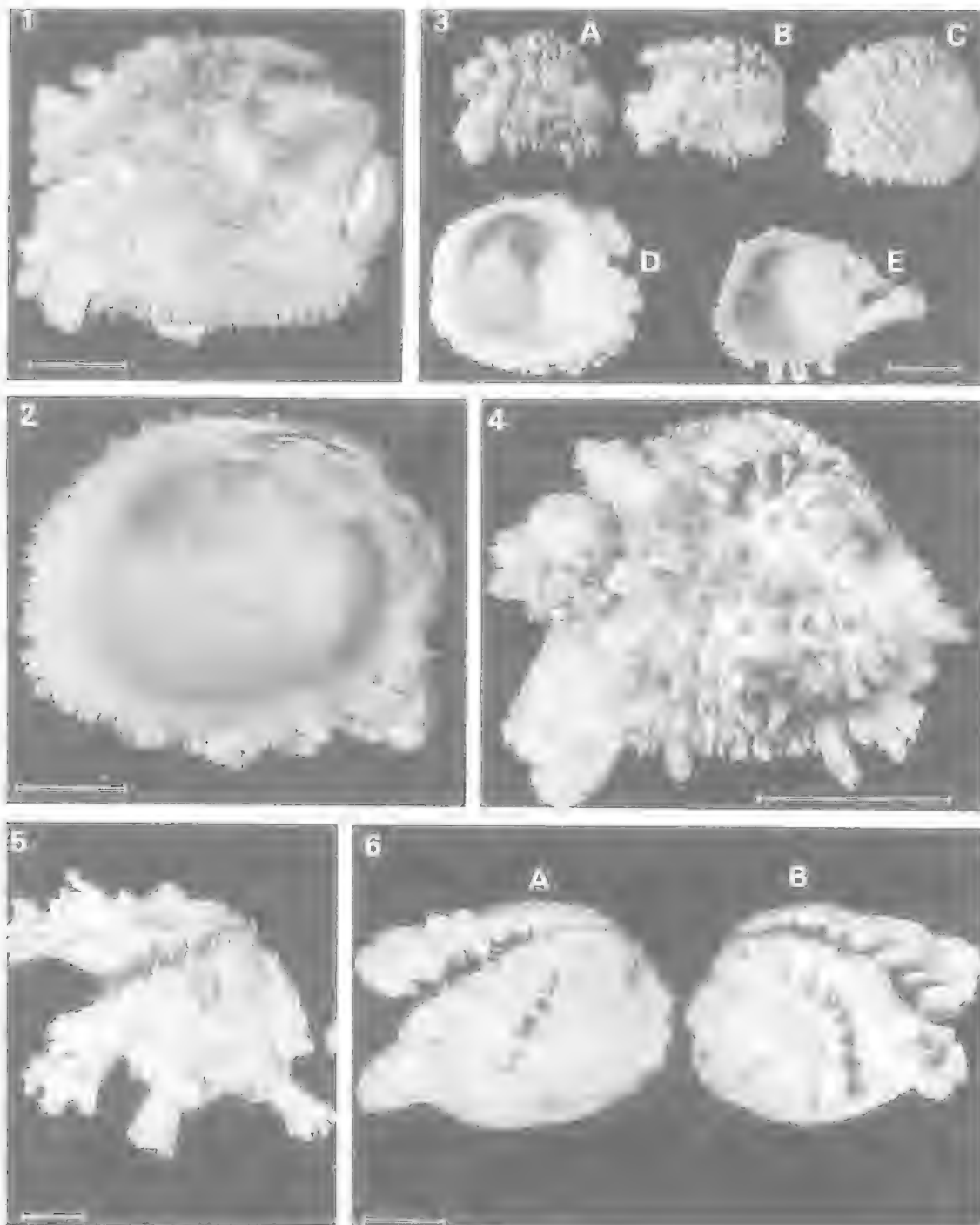
MATERIAL EXAMINED

HOLOTYPE: QMMO38412, 1 pv, Gulf of Carpentaria, 12°23.7'S, 140°41.1'E, dredged 58m, 26 Nov. 1991, S. Cook.

PARATYPES: AMC171008, 1 pv, Gulf of Carpentaria, 10°07.09'S, 141°48.36'E, dredged 47m, 1989, K Colgan; WAM83.92, 1pv, Timor Sea, 12°12'S, 129°15'E, dived 37m, 17 Nov. 1989, K. Colgan; QMMO38410, QMMO38411, 2pv, Gulf of Carpentaria, 13°07'S, 141°41'E, dredged 53.5m, 29 Nov. 1991, S. Cook.

DIAGNOSIS

Shell elongate-ovate; solid; small to moderately large; valves unequal and inequilateral; umbones prosogyrate. Externally, top (right) valve



FIGS 1-6. 1-4, *Chama isaacooki* sp.nov. 1, holotype (QMMO38412), external view of rv showing two broad bands of foliaceous spines posteriorly. 2, holotype (QMMO38412), internal view of lv showing teeth, crenulate margins and ligament. 3A,B,E, external (rv) and internal (lv) views of paratypes (A,E, WAM83.92; B, AMC171008); 3C,D, external and internal of specimen from Lamprell Collection. 4, external view of paratype (AMC171008) showing ribbed sculpture of broad spines. 5, *C. lazarus* Linnaeus, external view of rv, showing broad, foliate spines, Gove, NT. 6, *C. pulchella* Reeve. A, external view of top valve (rv), Torres Strait, NQ; B, external view of top valve (lv), Hervey Bay, SEQ. All scale bars = 10mm.

TABLE 1. Measurements (mm) of type series.

	L	H	W
Holotype: QMM03-412, lpx	36.8	37.5	25.1
Paratype: AMC171008, lpx	28.5	21.4	16.5
Paratype: WAM83 92, lpx	26.9	21.1	14.6

convex, densely ornamented with rows of hollow spines radiating from the umbonal area. Spines erect or curved, ribbed and broad terminally. Posteriorly the spines become leaf-shaped and organized into two loosely defined rows, separated by smaller, vaulted spines. Externally, bottom (left) valve deeply convex and densely ornamented with vaulted spines which frequently fuse laterally to form concentric foliations. Posterior margin with small non-fused spines. Internally, margins of both valves finely crenulate. Adductor scars elongate-ovate, prominent, anterior larger than posterior. Hinge plate featuring one large, broad cardinal and one posterior (remote) lateral tooth per valve. External colouration white with orange to purple-brown blotches: spines white, purple or pink with a dark spot at the base. Internal colouration white, often with large purple blotches, particularly in young specimens. Ligament brown, elongate, parivincular.

Sample size: 8 pv. Length:height ratio — range 1:1-1:0.73; mean 1:0.86. Length:width ratio — range 1:0.75-1:0.51, mean 1:0.65.

HABITAT AND DISTRIBUTION

Attached to living *Spondylus*, *Cardita* and *Crassostrea* in the Arafura Sea, Torres Strait and Gulf of Carpentaria at depths of 10 to 58m.

REMARKS AND COMPARISONS

Valve ornamentation, particularly the shape and arrangement of the spines, and the consistent presence of a dark spot at the base of each spine (spot frequently absent near margin) immediately distinguish *Chama isaacooki* from others of the genus. The degree of spine preservation in exposed reef dwelling species is often poor; hence unworn juvenile material has been examined in addition to adult shells. Two prominent, posterior rows of broad spines are also present in *C. pulchella* Reeve, 1847 (Fig. 6), *C. limbula* Lamarek, 1819 (Fig. 7B), *C. fibula* Reeve, 1846 (Fig. 8) and *C. plinthota* Cox, 1927 (Fig. 7A) but not in *C. lazarus* Linnaeus, 1758 (Fig. 5), *C. pacifica* Broderip, 1834 (Fig. 9A), *C. asperella* Lamarek, 1819 (Fig. 9C) or *C. ruderalis* Lamarek, 1819 (Fig. 9B). *C. lazarus*, *C. pulchella* and *C. ruderalis* differ from *C. isaacooki* and other Australian

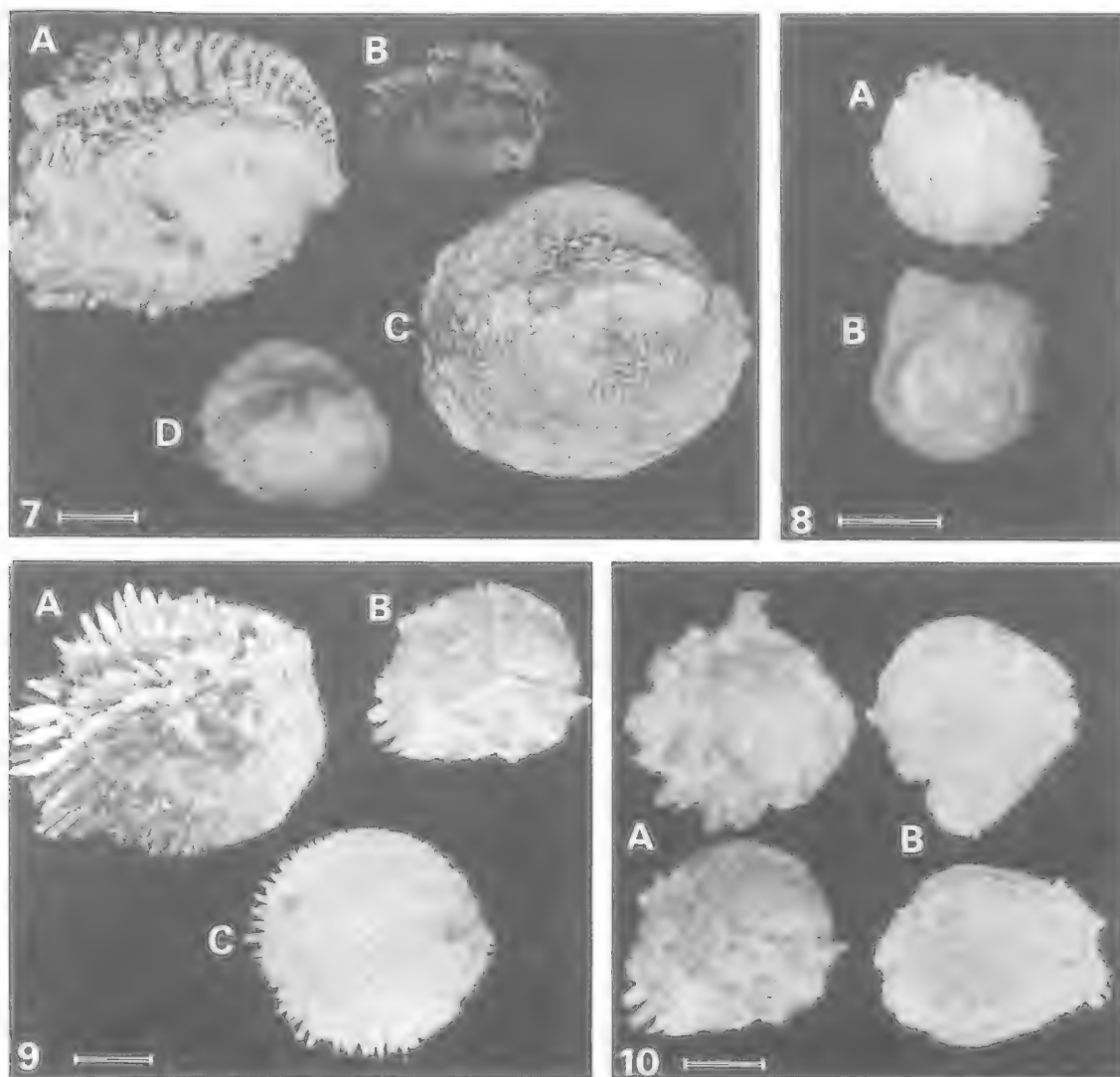
chamids by totally or almost totally lacking sharp spines.

KEY TO THE AUSTRALIAN CHAMIDAE

- 1a. Spines broad only, often fused to form lamellae 2
- Spines sharp or a mix of broad and sharp, broad spines never fused to form lamellae 3
- 2a. Spines equally developed across valve *C. lazarus*
- Spines inequally developed across valve *C. pulchella*
- 3a. Two prominent rows of broad spines dorso-posteriorly 4
- Two dorso-posterior rows of spines poorly developed or not distinguishable 5
- 4a. Valve with strong transverse corrugations dorso-posteriorly *C. plinthota*
- Valve without strong transverse corrugations 6
- 5a. Spines equally developed across valve 7
- Spines inequally developed across valve 8
- 6a. Valve margin finely crenulate ... *C. isaacooki*
- Valve margin smooth *C. limbula*
- 7a. Valve white, almost circular, strongly convex usually with rose-coloured umbone *C. asperella*
- Valve usually purple dorso-posteriorly, slightly elongate, weakly convex, umbone purple *C. fibula*
- 8a. Spines raised, organized into clearly defined radial rows *C. pacifica*
- Spines prostrate, not organized into well defined rows *C. ruderalis*

NOTES ON THE GENUS PSEUDOCHAMA ODHNER, 1917

Within the family Chamidae, attachment to the substrate may involve either the left valve (often referred to as the 'normal' condition) or the right valve (the 'inverse' condition) (Odhner, 1919; Cox, 1969). Early workers such as Broderip (1835) and Reeve (1846-7) indicated that both conditions may occur in the same species (for example *Chama pulchella*). Odhner (1917) disagreed and erected the genus *Pseudochama* for chamids attaching via the right valve, thereby reserving the genus *Chama* exclusively for species showing left valve attachment. He supported this division by drawing attention to differences in hinge teeth, the nepionic shell and anatomy between *Pseudochama* and *Chama* (see Odhner, 1919 for details). Although a number of recent authors have since accepted Odhner's opinion



FIGS 7-10. 7A, external view of top valve (rv) of *Chama plinthota* Cox (note strong transverse corrugations), Palm I., NEQ; 7B,C, external views of top valves (rv) of *C. limbula* Lamarck (B, immature, Fantome I., NEQ; C, One Arm Point, NWA); 7D, external view of top valve (rv) of *C. fibula* Reeve, Turkey Beach, MEQ. 8A, external view of top valve (rv) of *C. fibula*, Turkey Beach, MEQ; 8B, top valve (lv) of *C. fibula*, Redcliffe, SEQ. 9A, external view of top valve (rv) of *C. pacifica* Broderip, Swain Reefs, MEQ; 9B, external view of top valve (rv) of *C. ruderalis* Lamarck, Spencer Gulf, SA; 9C, external view of top valve (rv) of *C. asperella* Lamarck, Gloucester I., MEQ. 10A, top valves (rv) of two specimens of *C. ruderalis*, Spencer Gulf, SA; 10B, top valves (lv) of two specimens of *C. ruderalis*, Spencer Gulf, SA. All scale bars = 10mm.

that the valve of attachment can be used to determine generic placement (e.g. Keen, 1969; Del-saerdt, 1986), others have maintained the earlier Broderip-Reeve view that left and right valve attachment may occur in the same species (Lamy, 1927; Cotton, 1961; Lamprell & Whitehead, 1992).

During the present study we observed both left and right valve attached specimens in *Chama pulchella*, *C. fibula*, *C. limbula* and *C. ruderalis*. Typically the left valve is favoured but in *C. limbula* the ratio of left versus right attached specimens may approach 1:1 (Cotton, 1961). Although Odhner (1919: 11,17) accepted that certain chamids showing right valve attachment and

those showing left valve attachment may appear strikingly similar to each other in external colouration, sculpture and even attached valve dentition, he maintained that such similarity was due to convergence (pp.21,22) and that right valve attachment consistently differentiated *Pseudochama* from *Chama*. He therefore held that no species of Chamidae exhibited both left and right valve fixation. Odhner stressed differences in dentition between *Pseudochama* and *Chama*, but dismissed the possibility that any similarity in the arrangement of teeth between left and right attached valves could be the result of hinge teeth 'inversion' (= transposition). According to Cox (1969: N57) transposition of the hinge teeth in chamids 'goes hand-in-hand with reversal of the valve of fixation'.

Cox cited other examples of hinge teeth transposition in living and fossil taxa and in fact recommended that the Bernardian system of tooth notation (used throughout Odhner's work) not be applied in cases of tooth transposition at least until shell ontogeny has been examined in these taxa. In fact even Odhner stated that in various species of *Chama* (sensu Odhner) the details of hinge teeth may vary significantly through accentuation, suppression or addition of teeth (Odhner, 1919: 11). Yonge (1967), who made a detailed study of chamid anatomy, shell dentition and shell growth patterns, concluded that the process of cementation determined the morphology of the hinge teeth and valve profile in this family (significantly, Yonge examined both left and right valve attached specimens of *Chama pellucida* and *Pseudochama exogyra*). He supported the claim of Munier-Chalmas (1882) that free and attached valves of left valve attached specimens were mirror-images of the valves of right valve attached specimens. For this reason Yonge, like Munier-Chalmas, suggested recognizing 'free' and 'attached' valves rather than 'left' and 'right' and the application of non-Bernardian notation for Chamidae. Subsequently Yonge (1979) reverted to usage of 'left' and 'right' valves in discussing cementation in chamids (among other bivalves), but reiterated his earlier conclusion that genera within the family cannot be recognized by the valve of attachment (Yonge, 1979:100, in fact stating that 'There is no valid reason for separating the species into two genera'). By strict application of Odhner's valve of attachment rule (that is, all *Pseudochama* attach via the right valve), it would be necessary to hypothesize that left valve attached *Chama limbula*, *C. ruderalis*, *C. pulchella*

and *C. fibula* each coexist with a conchologically similar, but right valve attached species of *Pseudochama*. However, in view of the fact that hinge teeth transposition has now been well demonstrated in a number of heterodont groups (Cox, 1969), and after considering Yonge's (1967, 1979) findings that cementation has had an overriding effect on hinge teeth and valve morphology in the Chamidae, we conclude that a number of chamid species are truly capable of attaching by the left or the right valve. Any observable differences in dentition between left and right 'free' valves and left and right 'attached' valves should therefore be viewed as the result of transpositional effects.

The remaining features cited by Odhner (1917, 1919) as being diagnostic of *Pseudochama* — nepionic shell sculpture and morphology and/or position of the stomach caeca and the nephridia — seem worthy of detailed investigation. It would, for example, be interesting to determine whether such features occur in right valve attached specimens of *Chama limbula*, *C. fibula*, *C. ruderalis* and *C. pulchella*, particularly the latter which Odhner (1917) named *Pseudochama similis*. Should this not be the case, then the basis for the genus *Pseudochama* would have to be reassessed.

ACKNOWLEDGEMENTS

We would like to thank Mr Steve Cook, Queensland Museum for providing specimens of *Chama isanooki* for this study. Mr Ian Loei (Australian Museum) and Ms Sue Boyd (Museum of Victoria) provided access to collection material in their charge. Mr and Mrs Ivan Marrow (Melbourne) also allowed one of us (KL) the opportunity to examine specimens in their collection. This study was supported financially by an Australian Research Fellowship (to JH).

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A NEW CAVERNICOLOUS HARVESTMAN FROM LAVA TUBE CAVES IN TROPICAL AUSTRALIA (ARACHNIDA: OPILIONES: PHALANGODIDAE)

GLENN S. HUNT

Hunt, G.S. 1993 06 30: A new cavernicolous harvestman from lava tube caves in tropical Australia (Arachnida: Opiliones: Phalangodidae). *Memoirs of the Queensland Museum* 33(1): 217-219. Brisbane. ISSN 0079-8835.

Zalmoxis lavacaverna sp.nov. is from lava tube caves in the Mt Surprise area, north Queensland. It is the first cave-adapted harvestman to be described from tropical Australia. Troglomorphies include depigmentation, eye reduction, and elongation of appendages and spines on pedipalp. □ Arachnida, Opiliones, Phalangodidae, *Zalmoxis lavacaverna*, new species, cavernicolous, tropics, Australia.

Glenn S. Hunt, Australian Museum, PO Box A285, Sydney South, New South Wales, 2000, Australia; 13 July, 1992.

Hitherto, no harvestmen displaying cave adaptations (troglomorphies) have been described from caves in tropical Australia. *Zalmoxis lavacaverna* sp.nov. inhabits lava tubes in inland northern Queensland and shows depigmentation, some eye regression, elongation of spines on the pedipalp and elongation of appendages.

Elsewhere in Queensland, a cave adapted species has been recorded from Hercules Cave in the limestone tower karst region of Chillagoe (Howarth, 1988). This has proved to be another species of *Zalmoxis* but its description will await the discovery of a male.

Z. lavacaverna belongs to the family Phalangodidae, a group with many cavernicolous representatives in the Northern Hemisphere (e.g. Vandel, 1965; Briggs, 1968), though these are not closely related to *Zalmoxis*. Two troglomorphic phalangodids in the genus *Chondrobunus* have, however, been recorded from a limestone cave in New Guinea (Smith, 1980). The Phalangodidae, together with the Assamiidae, are tropical elements that replaced the older, more temperate families as Australia drifted northwards and established biological contact with Asia.

The temperate caves of southern Australia are populated by species of Triaenonychidae, predominantly the genera *Hicknanoxymma*, *Holonuncia* and *Lomanella* (Hunt, 1990, 1992; Hunt and Hickman, in press). These southern caves seem to support higher numbers of cavernicolous harvestmen, though this may be a consequence of more collecting and research.

Environmental parameters and faunal diversity of the lava tube caves are discussed by Howarth (1988) and Howarth & Stone (1990). He (1988) believed the biospeleological potential of tropical

caves in Australia was only just beginning to be appreciated.

Abbreviations. BMH=Bishop Museum, Hawaii; QM=Queensland Museum, Brisbane; BL=body length, BW=maximum body width, SL=scute length, CW=maximum carapace width, PFL=pedipalp femur length, FIV=femur IV length, CSL=cheliceral second segment length.

Zalmoxis lavacaverna sp.nov. (Fig. 1)

MATERIAL EXAMINED

HOLOTYPE: QM S20731, Queensland, Collins Two-Ten Cave, Spring Creek Station, Mt Surprise, 21 Jan 1989, M. Ashe, F.G. Howarth & H. Hoch, male.

PARATYPES: QM S20732, same data, female; BMH, same data, male & female.

OTHER MATERIAL: QM S20733, Queensland, Long Shot Cave, Spring Creek Station, Mt Garnet, 20 Jan 1989, F.G. Howarth, M. Ashe, H. Hoch & D. Irvin, male; QM S20734, same data, juvenile.

DIAGNOSIS

Cavernicolous. Depigmented, eyes reduced, 5 segments in tarsus IV.

DESCRIPTION

Male. Body. BL 3.10-3.15, SL 2.97-3.11, CW 1.04-1.10, BW 1.92-2.03. Depigmented, colour straw yellow to yellow-orange, appendages likewise. Anterior margin below with a process between chelicerae and between each chelicera and pedipalp, anterior margin above with 2 tubercles above each pedipalp coxa. Eyemound well developed, rising steeply a short distance behind anterior margin, armed with 1-3 tubercles, sloping less steeply posteriorly. Eye small, set low on

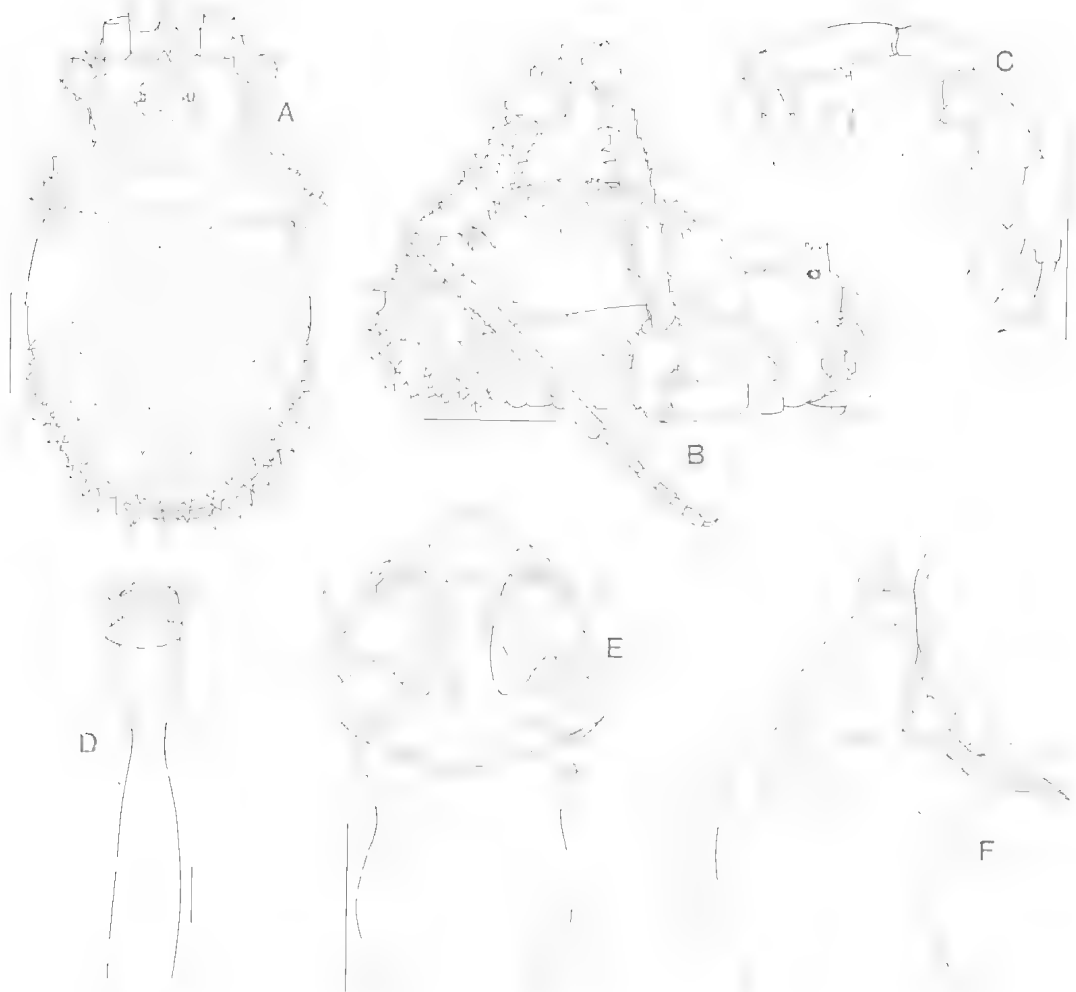


FIG. 1. *Zalmoxis lavacaverna* sp. nov., holotype male. A, body, dorsal; B, body, lateral, with leg IV; C, pedipalp, retrolateral; D, whole penis, ventral; E-F, apical part of penis, ventral and lateral. Scale bars: A-C = 1.0mm; D-F = 0.1mm.

eyemound, surrounded by small halo of pigmentation. Carapace with a few small tubercles as shown (Fig. 1A). Tergal areas 1-5 bearing a transverse row of tubercles or spines near their posterior margin, spines on TA 4 and 5 largest; TA1 - TA4 with second more anterior row composed of granules; TA5 narrow and without secondary row. The 3 free tergites each with row of strong spines; anal operculum and posterior sternites also carrying strong tubercles/spines (Fig. 1B).

Chelicera. Second segment with tiny setose granulations; CSL 0.80-0.84.

Pedipalp. PFL 0.64-0.66; femur with a two closely spaced proximoventral spines (Fig. 1C),

a smaller spine ventrally at about 0.66 femur length, and a prolateral spine at about 0.75 femur length. Patella with a prolateral spines in distal half; tibia with 3 pro- and 3 retrolateral spines, most distal retrolateral spine small, remaining two retrolateral spines larger than prolateral spines. Tarsus with two pro- and two larger retrolateral spines. Setae of all spines very long. Claw subequal to tarsus.

Legs. FIV 2.20-2.34 Femora with granules enlarging to tubercles/spines on ventral surface; spines particularly strong on femur IV. Tibia IV with strong subdistal ventral spine, spines distal to it may be subequal to or stronger than other

ventral spines; otherwise patella IV to metatarsus IV coarsely tuberculate. Tarsal formula 3,5-6,5,5.

Penis. A marked ventral shelf-like projection bears 4 pairs of setae, 1 mesial pair placed close together, 2 pairs more laterally, and 1 seta inserted on each side in dorsolateral projection of shelf. 2 mesial pairs of setae are placed more distally, setae further apart than proximal mesial pair. One small pair placed below (proximal to) shelf on ventrolateral margin of penis.

Female. Differs from male in the following: much smaller, BL 2.23-2.53, SL 2.12-2.31, BW 1.54-1.57, PFL 0.53-0.57, FIV 1.52-1.54. Body and legs with more subdued spination, large distal spine on tibia IV lacking. Tarsal formula 3,5,5,5.

VARIATION

Spination of the eyemound varies — eyemounds with 1 spine appear more conical. The strong spine on tibia IV in males varies in strength.

COMMENTS

On the basis of penis structure and spination of the body, *Z. lavacaverna* seems closely related to *Z. cardwellensis* Forster, 1955, which occurs in the coastal ranges directly to the east. It differs from *Z. cardwellensis* in being depigmented, having much longer appendages, a less bulbous femur IV, and 5 instead of 6 segments in tarsus IV. The female of both species is much smaller than the male. The undescribed troglomorphic species from Hercules Cave, Chillagoe, differs from *Z. lavacaverna* in having a more conical eyemound, more subdued spination of body and legs, and 6 rather than 5 segments in tarsus IV.

ETYMOLOGY

The specific epithet is formed by a latinised combination of two nouns, lava and cavern, descriptive of the species habitat.

NATURAL HISTORY

The species was taken well inside the lava tube caves where 98-100% humidities prevail (Howarth, 1988). Howarth regarded the species as 'possibly a troglobite'. The caves support a very large troglobitic and troglophilic fauna because tree roots and bat guano provide a steady flow of energy and nutrients to the community.

DISTRIBUTION

North Queensland; Long Shot and Two-Ten Caves, Collins lava tube system, Mt Surprise area. It does not seem to occur in the Bayliss lava tube, 30km to the NW, despite this cave having a

rich troglobitic fauna (Howarth & Stone, 1990). This supports the view that *Z. lavacaverna* is an obligate cavernicole incapable of long dispersals across the surface.

ACKNOWLEDGEMENTS

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NEW RECORD OF *LERISTA ALLANAE* (SQUAMATA: SCINCIDAE). *Memoirs of the Queensland Museum* 33(1): 220. 1993:- *Lerista allanae* (Longman, 1937) was described from 3 specimens from Retro Station, near Capella. Additional material (Greer, 1987; Ingram & Raven, 1991) indicated a range through much of central and central eastern Queensland. However, Couper & Ingram (1992) recognised two species, the more widespread *L. colliveri* Couper & Ingram, 1992 and *L. allanae* restricted to a small area between Clermont and Capella (30 km in N-S direction) and 32 km west of Capella. The latter was known from 9 specimens at 3 localities; it had been collected most recently in 1960 and recent searches in the same area have not added to these numbers. They concluded that the species was endangered, using the criteria of Ingram & Raven (1991:337).

In the South Australian Museum I located a specimen of *L. allanae* (R2823) from Logan Downs Station (22°23'S, 147°56'E), 56 km NE of the previously known range. It was collected by H. Womersley and registered on 16 November 1948. The collection date is not preserved with the specimen.

The specimen, an adult male (snout-vent length 72 mm) with turgid testes 4.5 mm long and opaque deferent ducts, agrees closely with the description of Couper & Ingram (1992) in most aspects of size and scalation, although some differences are: left hind limb missing; right hind limb monodactyle with 6 subdigital lamellae; nuchals (paravertebral scales on nape overlapping 4 or more scales) absent; second supraocular

on right side fused with right frontoparietal; superciliaries 6 in an unbroken row; infralabials 5; primary temporal present. Apparent differences in numbers of subdigital lamellae superciliaries may reflect different reference points rather than real differences. The specimen is faded and the colour pattern only faintly discernible.

I thank Mark Hutchinson for allowing access to South Australian Museum facilities.

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COMMON NAMES FOR QUEENSLAND FROGS

G.J. INGRAM, A.E.O. NATTRASS AND G.V. CZECHURA

Ingram, G.J., Nattrass, A.E.O. & Czechura, G.V. 1993 06 30: Common names for Queensland frogs. *Memoirs of the Queensland Museum* 33(1): 221-224. Brisbane, ISSN 0079-8835.

In Queensland, there has been a great increase in public interest in frogs. However, communication about frogs has been hampered by the lack of common, or English, names for the species. This checklist attempts to rectify the problem of communication by allocating a distinct common name to each species. The names are based on our experience of the frogs in the wild and familiarity with common names already in use. □ *Anura*, frog, common name, nomenclature, checklist, Queensland.

Glen Ingram & Greg Czechura, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; Ric Nattrass, 25 Warwick Court, Bellbird Park, Queensland 4300, Australia; 29 April, 1993.

In recent years there has been a great increase in public interest and concern regarding Queensland's native frogs. Several amateur societies have now been established throughout the State to watch, study or restore populations of frogs. Disappearance and possible extinction of several species in the wild and wider declines of others as a result of urban-sprawl have catalysed growing public fascination. 'Frog experts' are now in great demand to provide information about Queensland's frog fauna to both the public and media. However, scientists and naturalists are experiencing difficulties in communication because most frogs are only known by their scientific names; the media and public are reluctant to use these.

Some attempts have been made to introduce common, or English, names for popular usage (Moore, 1961; Clyne, 1969; Barker & Grigg, 1977; Ingram, 1983; Cogger, 1992 & earlier editions; Tyler, 1992). Not all of these efforts were comprehensive or not all the suggested names were adopted. Most suggestions have been based on literal translations of the latin nomenclature and this has often led to common names that are inappropriate, unwieldy or obscure. For example, *Litoria rubella* has been assigned the names 'Purple Treefrog' and 'Red-purple Treefrog' even though very few individuals are purple. And, inappropriately, it has also been called 'Desert Treefrog' even though it is commonly found in habitats other than desert. For many general users, the names recommended by scientists simply lack the 'colour' and 'descriptiveness' of the common names assigned to, for example, hummingbirds as in Sibley & Monroe (1990).

The following list—which has been developed from field experience, common names already in

use and discussions with interested parties—attempts to redress this imbalance by allocating a distinct common name to each species that occurs in Queensland. Common names should reflect some distinctive attribute of a taxon, or the place where they live, so that it is appropriate in most, if not all, contexts. As well, it should not create a misleading preconception of appearance. Furthermore, we feel it is desirable that designations using 'toad' only refer to the introduced *Bufo marinus*. Thus species of *Uperoleia* are herein referred to as 'gungans' from an aboriginal name (see Ingram & Corben, 1975) and not as 'toadlets'. 'Toadlet' should only be used to describe juvenile *B. marinus*.

In choosing and framing English names, we have followed the principles of Royal Australasian Ornithologists Union (R.A.O.U., 1978). Scientific names follow Ingram (1991) with addition of *U. altissima* Davies, Watson, McDonald, Trenerry & Werren, 1993.

CHECKLIST OF QUEENSLAND FROGS

TOADS BUFONIDAE

Bufo Laurenti, 1768
CANE TOAD *B. marinus* (Linnaeus, 1758)

TREEFROGS AND RELATIVES HYLIDAE

Cyclorana Steindachner, 1867
NORTHERN SNAPPING FROG *C. australis* (Gray, 1842)
SUPERB COLLARED-FROG *C. brevipes* (Peters, 1871)
DESERT COLLARED-FROG *C. cultripes* Parker, 1940
WESTERN COLLARED-FROG *C. maini* Tyler & Martin, 1977

LITTLE COLLARED-FROG *C. manya* Van Beurden & McDonald, 1980
 EASTERN SNAPPING-FROG *C. novaehollandiae* Steindachner, 1867
 WATER-HOLDING FROG *C. platycephalus* (Günther, 1873)

Litoria Tschudi, 1838

GREENSTRIPE FROG *L. alboguttatus* (Günther, 1867)
 NORTHERN SEDGEFROG *L. bicolor* (Gray, 1842)
 GREEN-THIGHED FROG *L. brevipalmata* Tyler, Martin & Watson, 1972
 GREEN TREEFROG *L. caerulea* (White, 1790)
 SOUTHERN ORANGE-EYED TREEFROG *L. chloris* (Boulenger, 1893)
 COOLOOLA SEDGEFROG *L. cooloolensis* Liem, 1974
 SANDSTONE FROG *L. coplandi* (Tyler, 1968)
 NORTHERN WATERFROG *L. dahliei* (Boulenger, 1896)
 BLEATING TREEFROG *L. dentata* (Keferstein, 1868)
 ELECTRIC TREEFROG *L. electrica* Ingram & Corben, 1990
 EASTERN SEDGEFROG *L. fallax* (Peters, 1880)
 WALLUM ROCKETFROG *L. freycineti* Tschudi, 1838
 GREEN-EYED TREEFROG *L. genimaculata* (Horst, 1883)
 GRACEFUL TREEFROG *L. gracilentata* (Peters, 1869)
 BUMPY ROCKETFROG *L. inermis* (Peters, 1868)
 WHITE-LIPPED TREEFROG *L. infrafrenata* (Günther, 1867)
 BROAD-PALMED ROCKETFROG *L. latopalmata* Günther, 1867
 STONY-CREEK FROG *L. lesueuri* (Duméril & Bibron, 1841)
 SCRUB ROCKETFROG *L. longirostris* Tyler & Davies, 1977
 ARMoured MISTFROG *L. lorica* Davies & McDonald, 1979
 PYGMY ROCKETFROG *L. microbelos* (Cogger, 1966)
 WATERFALL FROG *L. nannotis* (Andersson, 1916)
 STRIPED ROCKETFROG *L. nasuta* (Gray, 1842)
 TAWNY ROCKETFROG *L. nigrofrenata* (Günther, 1867)
 MOUNTAIN MISTFROG *L. nyakalensis* Liem, 1974
 WALLUM SEDGEFROG *L. olongburensis* Liem & Ingram, 1977
 PEACH-SIDED ROCKETFROG *L. pallida* Davies, Martin & Watson, 1983
 CASCADE TREEFROG *L. pearsoniana* (Copland, 1961)
 EMERALD-SPOTTED TREEFROG *L. peronii* (Tschudi, 1838)
 WHIRRING TREEFROG *L. revelata* Ingram, Corben & Hosmer, 1982
 COMMON MISTFROG *L. rheocola* Liem, 1974
 RED-EYED TREEFROG *L. rothii* (de Vis, 1884)
 NAKED TREEFROG *L. rubella* (Gray, 1842)
 NEW ENGLAND TREEFROG *L. subglandulosa* Tyler & Anstis, 1983

BLACK-SHINNED ROCKETFROG *L. tornieri* (Nieden, 1923)

LAUGHING TREEFROG *L. tyleri* Martin, Watson, Gartside, Littlejohn & Loftus-Hills, 1979

WHISTLING TREEFROG *L. verreauxii* (Duméril, 1853)

GIANT ROCKETFROG *L. woljulumensis* (Copland, 1957)

NORTHERN ORANGE-EYED TREEFROG *L. xanthomera* Davies, McDonald & Adams, 1986

Nyctimystes Stejneger, 1916

AUSTRALIAN LACE-LID *N. dayi* (Günther, 1897)

NARROW-MOUTHED FROGS
MICROHYLIDAE

Cophixalus Boettger, 1892

WINDSOR NURSERY-FROG *C. bombiens* Zweifel, 1985

TAPPING NURSERY-FROG *C. concinnus* Tyler & Davies, 1979

NORTHERN NURSERY-FROG *C. crepitans* Zweifel, 1985

BLOOMFIELD NURSERY-FROG *C. exiguus* Zweifel & Parker, 1969

PIPPING NURSERY-FROG *C. hosmeri* Zweifel, 1985

BUZZING NURSERY-FROG *C. infacetus* Zweifel, 1985

SOUTHERN NURSERY-FROG *C. mcdonaldi* Zweifel, 1985

TANGERINE NURSERY-FROG *C. neglectus* Zweifel, 19623

COMMON NURSERY-FROG *C. ornatus* (Fry, 1912)

CAPE YORK NURSERY-FROG *C. peninsularis* Zweifel, 1985

BOULDER NURSERY-FROG *C. saxatilis* Zweifel & Parker, 1977

Sphenophryne Peters & Doria, 1878

CRICKET CHIRPER *S. fryi* Zweifel, 1962

SHRILL CHIRPER *S. gracilipes* (Fry, 1912)

WHITE-BROWED CHIRPER *S. pluvialis* Zweifel, 1965

PEALING CHIRPER *S. robusta* (Fry, 1912)

PARENTAL-CARE FROGS AND RELATIVES
MYOBATRACHIDAE

Adelotus Ogilby, 1907

TUSKED FROG *A. brevis* (Günther, 1863)

Assa Tyler, 1976

AUSTRALIAN MARSUPIAL FROG *A. darlingtoni* (Loveridge, 1933)

Crinia Tschudi, 1838

CHIRPING FROGLET *C. deserticola* (Liem & Ingram, 1977)

BEEPING FROGLET *C. parinsignifera* Main, 1957

TORRID FROGLET *C. remota* (Tyler & Parker, 1974)

CLICKING FROGLET *C. signifera* (Girard, 1853)

WALLUM FROGLET *C. timmula* Straughan & Main, 1966

Kyarranus Moore, 1958

RED-AND-YELLOW MOUNTAIN-FROG *K. kundagungan*
Ingram & Corben, 1975

MASKED MOUNTAIN-FROG *K. loveridgei* (Parker,
1940)

Lechriodus Boulenger, 1882

BLACK-SOLED FROG *L. fletcheri* (Boulenger, 1890)

Limnodynastes Fitzinger, 1843

MARBLED FROG *L. convexiusculus* (Macleay, 1877)

GREY-BELLIED POBBLEBONK *L. dumerilii* Peters, 1863

BARKING FROG *L. fletcheri* Boulenger, 1888

ORNATE BURROWING-FROG *L. ornatus* (Gray, 1842)

STRIPED MARSHFROG *L. peronii* (Duméril & Bibron,
1841)

SALMON-STRIPED FROG *L. salmini* Steindachner, 1867

SPOTTED MARSHFROG *L. tasmaniensis* Günther, 1858

SCARLET-SIDED POBBLEBONK *L. terraereginae* Fry,
1915

Mixophyes Günther, 1864

GREAT BARRED-FROG *M. fasciolatus* Günther, 1864

FLEAY'S BARRED-FROG *M. fleayi* Corben & Ingram,
1987

GIANT BARRED-FROG *M. iteratus* Straughan, 1968

NORTHERN BARRED-FROG *M. schevilli* Loveridge,
1933

Neobatrachus Peters, 1863

RATTLING METAL-EYED FROG *N. aequilonius* Tyler,
Davies & Martin, 1981

TRILLING METAL-EYED FROG *N. centralis* (Parker,
1940)

EASTERN METAL-EYED FROG *N. sudelli* (Lamb, 1911)

Notaden Günther, 1873

HOLY CROSS FROG *N. bennettii* Günther, 1873

BROWN ORBFROG *N. melanoscaphus* Hosmer, 1962

RUBY-SPOTTED ORBFROG *N. nichollsi* Parker, 1949

Pseudophryne Fitzinger, 1843

RED-BACKED BROODFROG *P. coriacea* Keferstein,
1868

GREAT BROWN BROODFROG *P. major* Parker, 1940

Rheobatrachus Liem, 1973

SOUTHERN PLATYPUSFROG *R. silus* Liem, 1973

NORTHERN PLATYPUSFROG *R. vitellinus* Mahony, Ty-
ler & Davies, 1984

Taudactylus Straughan & Lee, 1966

SHARP-SNOURED DAYFROG *T. acutirostris* (Andersson,
1916)

SOUTHERN DAYFROG *T. diurnus* Straughan & Lee,
1966

EUNGELLA DAYFROG *T. eungellensis* Liem & Hosmer,
1973

EUNGELLA TINKERFROG *T. liemi* Ingram, 1980

KROOMBIT TINKERFROG *T. pleione* Czechura, 1986

NORTHERN TINKERFROG *T. rheophilus* Liem & Hos-
mer, 1973

Uperoleia Gray, 1841

TABLELAND GUNGAN *U. altissima* Davies, Watson,
McDonald, Trenerry & Werren, 1993

DESERT GUNGAN *U. capitulata* Davies, McDonald &
Corben, 1986

SANDY GUNGAN *U. fusca* Davies, McDonald & Cor-
ben, 1986

FLOODPLAIN GUNGAN *U. inundata* Tyler, Davies &
Martin, 1981

EASTERN GUNGAN *U. laevigata* Keferstein, 1867

STONEMASON GUNGAN *U. lithomoda* Tyler, Davies &
Martin, 1981

RED-SPECKLED GUNGAN *U. littlejohni* Davies, McDon-
ald & Corben, 1986

TORRES GUNGAN *U. mimula* Davies, McDonald &
Corben, 1986

CHUBBY GUNGAN *U. rugosa* (Andersson, 1916)

ORANGE-SHOULDERED GUNGAN *U. trachyderma* Tyler,
Davies & Martin, 1981

TRUE FROGS

RANIDAE

Rana Linnaeus, 1758

AUSTRALIAN BULLFROG *R. daemeli* Steindachner,
1868

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tions.

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SPERMATOLOGICAL EVIDENCE FOR THE TAXONOMIC STATUS OF *TRAPEZIA*
(CRUSTACEA: BRACHYURA: HETEROTREMATA)

B.G.M. JAMIESON

Jamieson, B.G.M. 1991 06 30: Spermatological evidence for the taxonomic status of *Trapezia* (Crustacea: Brachyura: Heterotremata). *Memories of the Queensland Museum* 33(1): 225-234, Brisbane, ISSN 0079-8835.

Features of the spermatozoon of *Trapezia* which are general for heterotremes and endorse its inclusion in the Heterotremata are: extension of the subacrosomal chamber almost to the anterior apex of the sperm; division of the acrosome contents into inner and outer zones; presence of an acrosomal ray zone at the periphery of the inner acrosomal zone; and presence of a thickened ring where the acrosomal capsule surrounds the base of the subacrosomal chamber. A feature shared with 'higher' heterotremes is the restriction of cytoplasm to the periacrosomal region, the arms being nuclear only; and loss of a posterior median process, containing chromatin, which is present in raninids and majids. Additional features which *Trapezia* shares with the Xanthidae (exemplified by Xanthinae and Chlorodiinae) and Panopeidae (exemplified by *Eurytium*) include the structure of the perforatorium, tapering anteriorly, with a fibrous core; and extension of the chromatin around the operculum, leaving only a raised central area of this exposed. Peculiar features of xanthids (Xanthinae, Chlorodiinae) and panopaeids which separate them from all other heterotremes, including *Trapezia*, are the dense 'xanthid ring' around the base of the subacrosomal chamber and, in xanthids, the additional peripheral zone outside the outer acrosomal zone. Presence of a presumed derivative of the xanthid ring in thoracotremes indicates that the Xanthidae s. strict. and panopaeids are near the base of the Thoracotremata and absence of the ring in *Trapezia* suggests that it (in the Trapeziidae) is the plesiomorphic sister- or neighbouring-taxon of the xanthid-panopaeid assemblage. An apomorphy of *Trapezia* is restriction of the acrosome ray zone to an annulus around the anterior region of the perforatorium. Presence of the ring or its derivatives indicates that although the xanthids, panopaeids, and such thoracotremes form a monophyletic group, the Xanthoidea is a paraphyletic group. □ Crustacea, phylogeny; spermatozoa, ultrastructure, *Trapezia*, *Pilodius*, *Eurytium*, *Mictyris*.

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Trapezia Latreille, 1825, is a genus of heterotreme crabs, the species of which are obligate symbionts of corals (Abele & Felgenhauer, 1982). The 'trapézides' of A. Milne Edwards, 1862, were given subfamilial rank, as the Trapeziinae, by Miers (1886) in the family Xanthidae of Macleay, 1838. This allocation of *Trapezia* was widely accepted. However, Guinot (1978) revived Ortmann's (1893) idea, subsequently abandoned, that a family Trapeziidae should be recognised. Within her Xanthoidea, Guinot (1978: 275) considered the Trapeziidae Miers to be a distinctive family equal in rank to the Xanthidae, and other xanthoid families (the Carpilidae, Menippidae, Platyxanthidae, Pilumnidae, Panopeidae and Geryonidae), a view supported by specialists on the genus *Trapezia* (e.g. Clark & Galil, 1988).

Despite objections that classification on larval characters conflicts with that on adult characters (Gurney, 1938; Lebour, 1944), studies of larval development have been considered to confirm

relationship of *Trapezia* with other xanthoid genera (Hyman, 1925; Wear, 1970; Rice, 1980; Martin, 1984). The classifications of Hyman (1925) and Wear (1970) suggested a special relationship of *Trapezia* to menippines and pilumnines (Menippidae and Pilumnidae sensu Guinot, 1978). Nevertheless, Guinot (unpublished) considers that the distinctive morphology of *Trapezia* may justify recognition of a distinct superfamily Trapezoidea.

The present study examines the ultrastructure of the spermatozoa of *Trapezia coerules* with a view to providing evidence of its relationships. For comparative purposes, micrographs are included of the sperm of the xanthid *Pilodius areolatus* and the thoracotreme *Mictyris longicarpus* (Mictyridae) and brief reference (in the Discussion) is made to the sperm of the panopaeid *Eurytium limosum* (Say) (Jamieson & Abele, unpublished). Published descriptions of xanthoid sperm are limited to a brief description for *Menippe mercenaria* (Menippinae) by Brown

(1966) in an unpublished doctoral thesis; a diagram of the sperm of *Atergatis floridus* (Linnaeus) in a discussion of malaenostreacan phylogeny by Jamieson (1989c); detailed description of the sperm of *Atergatis floridus* (Xanthidae, Zosiminae), *Etisus laevimanus* Randall (Xanthidae, Etisinae), *Liagore rubromaculata* De Haan (Carpiliidae, incertae sedis) and *Pilodius areolatus* (H. Milne-Edwards) (Xanthidae, Chlorodiinae) by Jamieson (1989a); brief mention of *Eurypanopeus depressus* (Smith) and an SEM micrograph for *Eurytium limosum* (Say) (both Panopeidae) by Felgenhauer & Abele (1990) and a description for *Geryon fenneri* and *G. quinqueedens* (Geryonidae), by Hinsch (1988). It is unfortunate that no descriptions of spermatozoal ultrastructure exist for Pilumnidae and that the brief description for *Menippe mercenaria* by Brown (1966) in an unpublished doctoral thesis does not give sufficient detail for purposes of comparison, in view of the supposed relationship of these to *Trapezia*.

MATERIAL AND METHODS

Species examined for sperm ultrastructure are: *Trapezia coerulea* Rüppell, from Heron Island, Great Barrier Reef; the xanthid *Pilodius areolatus* (H. Milne-Edwards), from One Tree Island, Great Barrier Reef; the panopeiid *Eurytium limosum* (Say) (see Discussion only) from the vicinity of Talahassee, Florida, USA; and the thoracotreme *Mictyris longicarpus* Latreille (Mictyridae), from Moreton Bay, Queensland. The specimen of *Trapezia* used has been lodged in the collections of the Queensland Museum.

Small portions of testes of were fixed in 3% glutaraldehyde in 0.1M phosphate buffer (pH 7.4), with 6% sucrose, at 4°C, washed in buffer, post-fixed for 80 min in similarly buffered 1% osmium tetroxide, washed in buffer, dehydrated through an ascending ethanol series, and infiltrated and embedded in Spurr's epoxyresin. Thin sections were cut with a diamond knife on an LKB 2128 UMIV ultratome, collected on carbon stabilised collodion-coated 200 mesh copper grids, and stained by the Daddow method: for 0.5 min in Reynolds' lead citrate, 1 min in 6% aqueous uranyl acetate and a further 0.5 min in lead citrate, before rinsing in distilled water. Specimens were examined with a Hitachi 300 and a Jeol 100S transmission electron microscope operated at 80kV and 60kV respectively.

RESULTS AND COMPARATIVE REMARKS

The terminology adopted by Jamieson (1989a,b, 1991) will be employed in this account with the modification that the inner zone of the acrosome and the acrosome ray zone will be recognised as distinct layers, rather than being combined under the term inner dense zone. This modification of terminology will accommodate the condition in paguroid anomurans where the acrosome ray zone may form the widest layer of the acrosome. Although in Brachyura the acrosome ray zone is sometimes poorly delimited from or forms part of an inner dense zone, the two layers will therefore be recognised as the 'inner acrosomal zone' and the 'acrosome ray zone'. To minimise repetition of data from *Trapezia* in the Discussion, some comparison with archaebachyuran and other heterotreme crabs will be made in the Results. Comparison with thoracotremes will chiefly be reserved to the Discussion.

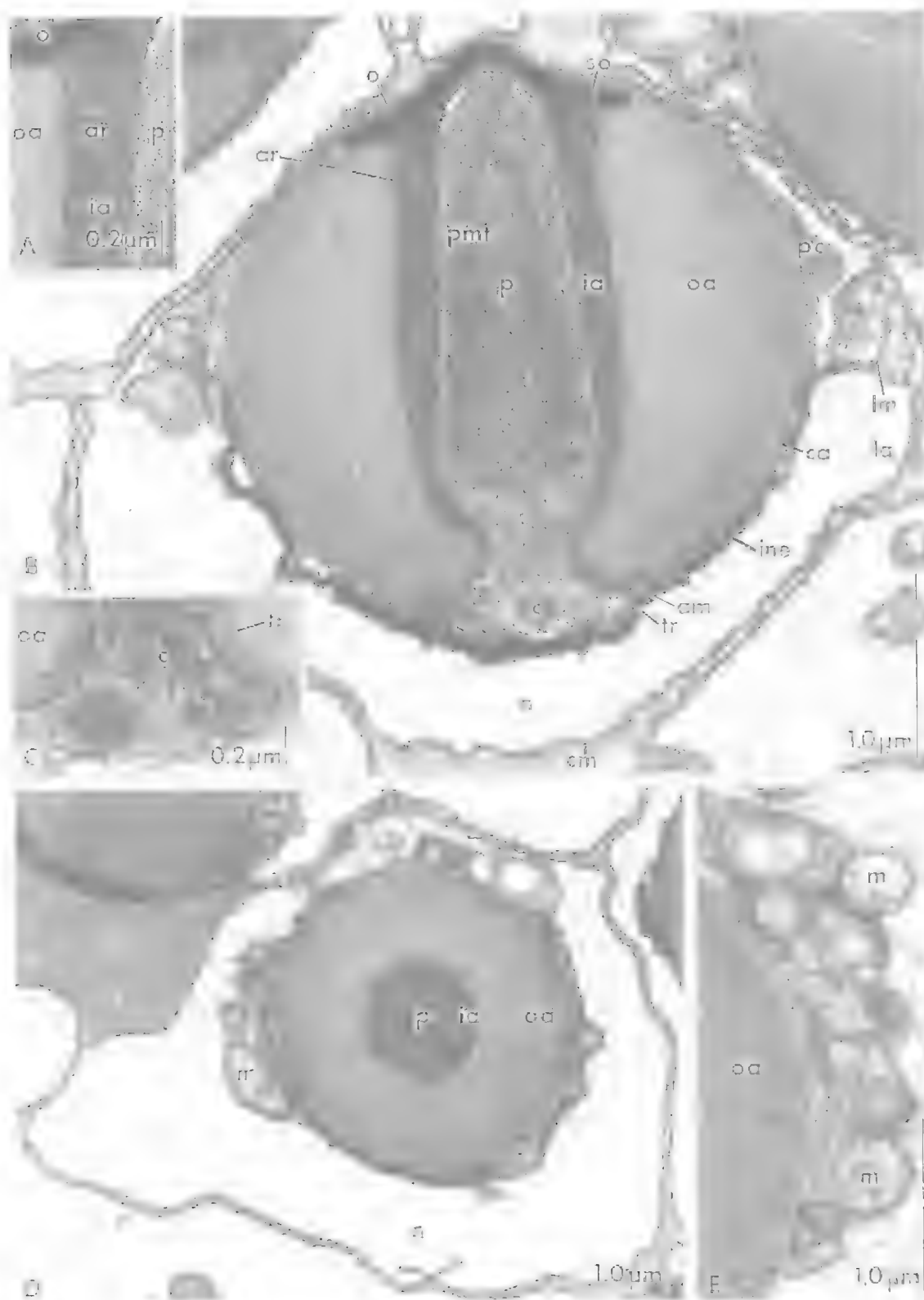
GENERAL MORPHOLOGY

The spermatozoon of *Trapezia coerulea* is illustrated from transmission electron microscopy in a line drawing (Fig. 1) and in micrographs (Fig. 2). For comparison with a xanthid and a thoracotreme, these are illustrated by micrographs of the sperm of *Pilodius areolatus* (Fig. 3) and the thoracotreme *Mictyris longicarpus* (Fig. 4).

The spermatozoon of *Trapezia coerulea* (Fig. 1) is spheroidal but slightly depressed anteroposteriorly and, like all decapod sperm, lacks a flagellum (Fig. 2B). This simple form is modified by the presence of broadly based lateral projections or 'arms'. From light micrographs, there are four arms, each with a length considerably surpassing the diameter of the sperm body. A plesiomorphic, chromatin-containing 'posterior median process', seen in *Ranina* and some majids, is absent. As is usual for brachyurans, the nucleus consists of diffuse, fibrous chromatin, and forms a cup surrounding the acrosome, a thin layer of cytoplasm intervening between nucleus and acrosome. The cytoplasm contains sparse mitochondria, some membranous (lamellar) structures of probable mitochondrial origin and, basal to the perforatorium, the two centrioles (Figs 2B,C,D).

ACROSOME

The subspheroidal core of the *Trapezia* spermatozoon consists entirely of the complex



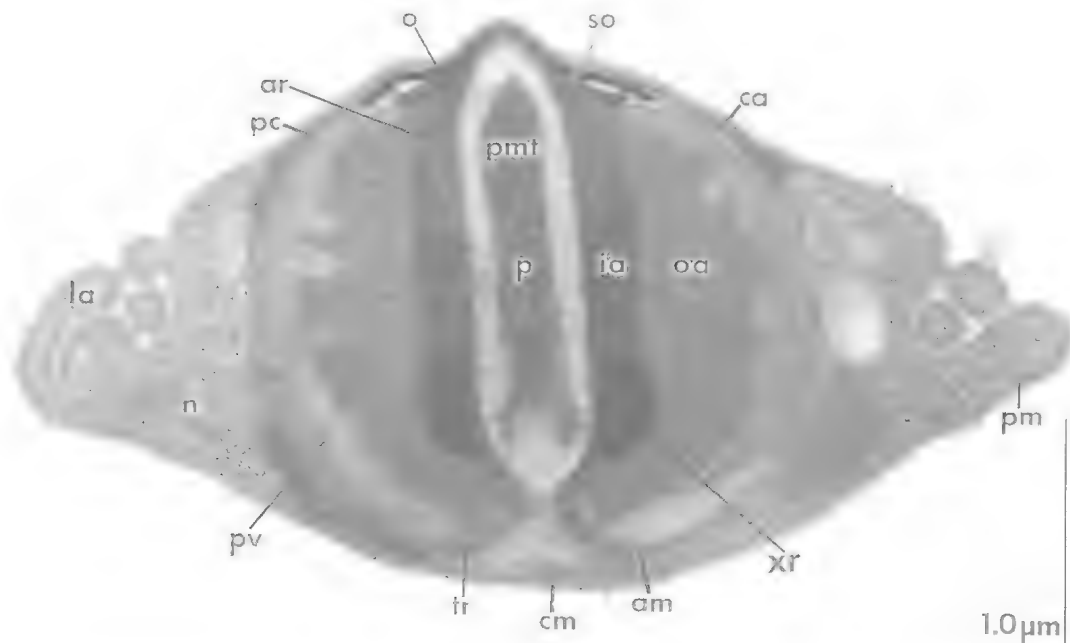


FIG. 3. Transmission electron micrograph of a longitudinal sagittal section of the spermatozoon of the xanthid *Pilodius areolatus*. Abbreviations: am = acrosome membrane; ar = acrosomal rays; ca = capsule; cm = cell membrane; ia = inner acrosomal zone; la = base of lateral arm; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pc = vestigial periacrosomal cytoplasm; pmt = microtubules of perforatorium; so = subopercular zone; tr = thickened ring; xr = xanthid ring.

margin of the outer dense zone peculiar to xanthids is ragged and deeply dissected (*Atergatis* and *Pilodius*) or slightly crenulated (*Etisus*) or almost smooth (*Liagore*).

At the anterior pole of the *Trapezia* acrosome, as in all other brachyurans and paguroids with the doubtful exception of *Pagurus bernhardus* (see Chevaillier, 1968), there is a dense caplike structure, the operculum (Fig. 2B), 1.3–1.5 μm wide (mean of 3 = 1.4 μm). As in *Portunus*, the operculum is imperforate whereas in *Ranina* and the majid *Menaethus monoceros* it is perforate (see Jamieson, 1991), although in some individual xanthid sperm it appears weakened apically (it is also perforate but is closed by an apical button in most of the investigated thoracotremes, Fig. 4A, see Discussion).

Below the operculum, as in many other crabs, a further, caplike structure of moderately electron dense material, the subopercular zone, separates the operculum and adjacent region of the capsule from the summit of the inner acrosomal zone and acrosome ray zone (Fig. 2B). In *Trapezia*, as in xanthids, the operculum extends laterally slightly beyond the acrosome ray zone. In contrast the operculum is limited in *Calappa* to the width of the ray zone while in portunids and dorippids it is more extensive as it also caps the outer acrosomal zone (see Jamieson, 1991).

At the opposite, posterior, pole the capsule is perforated by invagination of the acrosome membrane and capsule as a narrow orifice which opens into the columnar subacrosomal chamber. Unlike the *Ranina* sperm but like that of *Calappa*, portunids, *Neodorippe* and xanthids, a thickening of

FIG. 2. *Trapezia coerulea*. Transmission electron micrographs of the spermatozoon. A. Detail of acrosome ray zone. B. Longitudinal sagittal section. C. Detail of centriolar region. D. Transverse section shortly below the equator of the acrosome. E. Detail of the cytoplasmic layer in transverse section, showing mitochondria in various stages of degeneration. Abbreviations: am = acrosome membrane; ar = acrosomal rays; c = centriole(s); ca = capsule; cm = cell membrane; ia = inner acrosomal zone; ine = multilayered inner nuclear envelope; la = base of lateral arm; lm = contorted (lamellar) membranes; m = degenerating mitochondrion; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pc = vestigial periacrosomal cytoplasm; pmt = microtubules of perforatorium; so = subopercular zone; tr = thickened ring.

the capsule forms a 'thickened ring' on each side of the subacrosomal invagination (Fig. 2B).

SUBACROSOMAL REGION

In *Trapezia*, as in xanthids and other heterotreme (and thoracotreme) Brachyura, the subacrosomal material consists of a highly differentiated stout perforatorium that extends from the posterior perforation in the capsule to the vicinity of the operculum at the apex of the acrosome (Fig. 2B). The perforatorium in *Trapezia* is a stout cylinder, slightly tapering anteriorly, with a bluntly pointed tip and a posterior stalk constricted at the thickened ring. This form, together with differentiation of the perforatorium into a central dense fibrous core, is indistinguishable from that stated to be distinctive of xanthids (see *Pilodius*, Fig. 3) by Jamieson (1989a). In cross section, the perforatorium is seen to contain, as in xanthids and portunids (Jamieson, 1991) many circular profiles resembling microtubules though differing from typical microtubules in varying in size and in sometimes being irregular in section (Fig. 2D).

CYTOPLASM

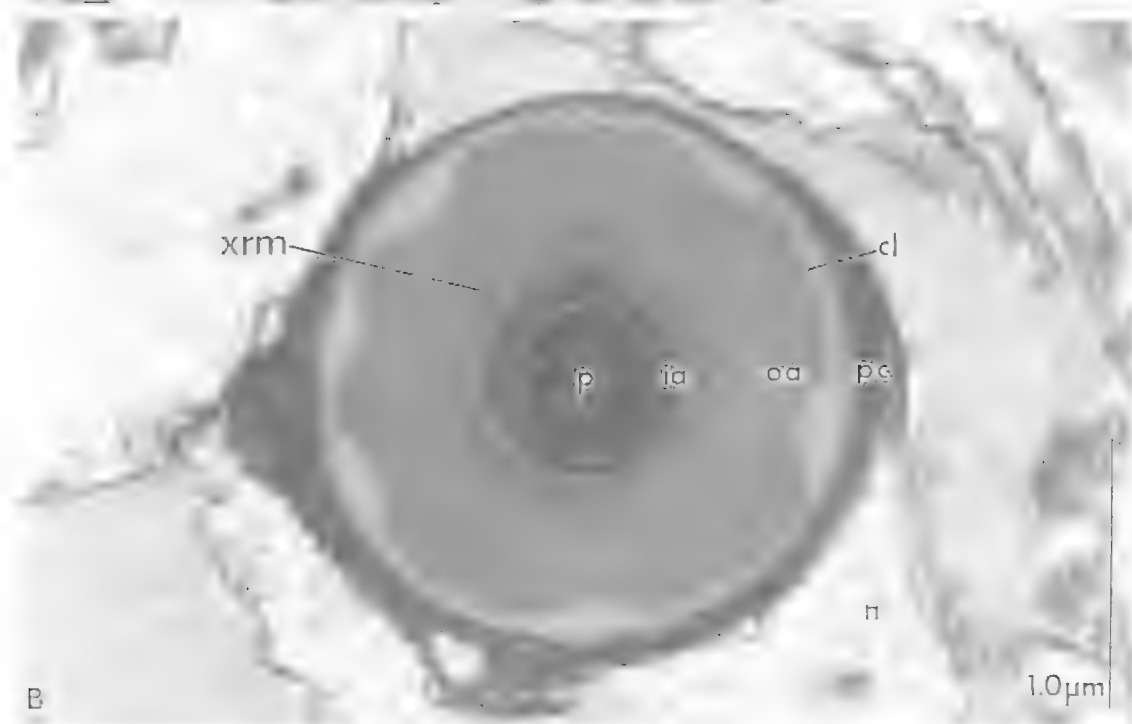
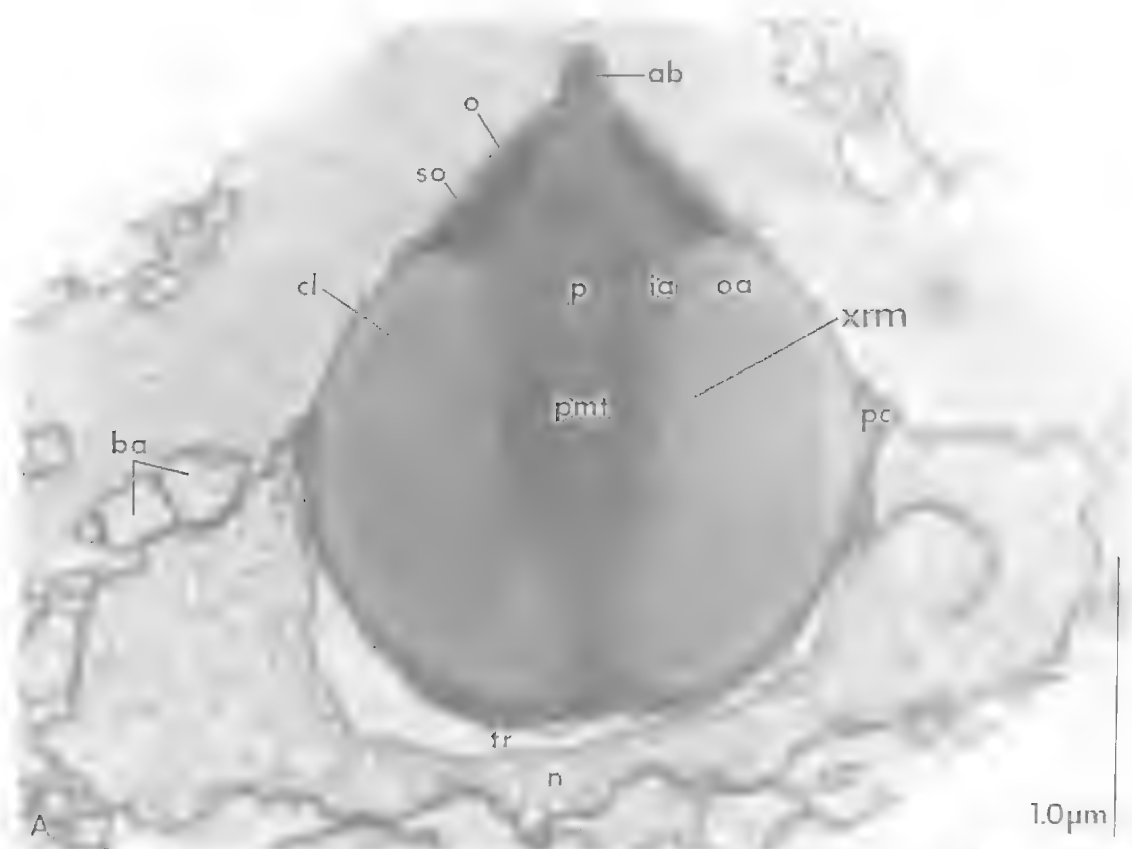
A thin layer of spermatozoal cytoplasm surrounds the acrosomal capsule. As in portunids, dorippids and xanthids the cytoplasm does not extend into the arms. In majids, in contrast, the cytoplasm extends into the lateral arms together with contained microtubules which are not discernible in the other heterotremes mentioned. In *Trapezia* the cytoplasm is enlarged anterolaterally on one side of the capsule and contains several subspheroidal and apparently degenerating mitochondria with sparse cristae (Figs 2D,E). The degree of representation of mitochondria is variable in other heterotremes, usually being negligible, though it is similar to that in *Trapezia* in the thoracotreme *Macrophthalmus crassipes* and the archaeobranchyuran *Ranina ranina* (see Jamieson, 1991). The postacrosomal cytoplasm, typical of brachyurans and well developed in *Trapezia*, contains two centrioles (Figs 2B,C), a plesiomorphic condition seen in majids, parthenopids, calappids, portunids, dorippids and *Macrophthalmus* but absent in xanthids (Fig. 3) and, usually, in thoracotremes (see Jamieson, 1991).

Contorted membranes are present among the mitochondria of the dilated region of the cytoplasm and in extensions of the cytoplasm into the chromatin (Fig. 1, 2B). These membranes are the equivalent of the sometimes better developed lamellar structure seen in other brachyuran sperm. In *Trapezia* some of the membranes are continuous with the multilaminar prenuclear membrane (see below) and also appear to be continuous with membranes of disintegrating mitochondria. It seems possible, therefore, that the multilaminar membrane is at least partly derived from mitochondrial membranes.

NUCLEUS

In *Trapezia*, as in xanthids, and other brachyurans, the nuclear material is located in the lateral arms and their branches (Fig. 2B) and in the cup-shaped structure around both the acrosome and its cytoplasmic sheath. The chromatin extends around the operculum, leaving only the raised central area of this exposed (Fig. 2B), as in xanthids, whereas in portunids and *Neodorippe* the operculum is not covered. The envelope between the chromatin and the basal cytoplasm is unusually well developed in *Trapezia* and is represented by a dense double membrane bounding the cytoplasm (the nature of which is obscure as it cannot be the plasma membrane). Posterior to this membrane, bounding the anterior face of the nucleus, a series of six or more dense membranes (inner nuclear membrane in Fig. 2B), make up a multilaminar membrane. In xanthids and *Portunus*, for instance, the nuclear envelope though retained is disrupted and is not multilaminar. Nevertheless, the multilaminar membrane in *Trapezia* is incomplete, as it ends anteriorly at the lamellar structures. The external, basal surface of the cell, is bounded by a dense membrane, which may represent fused nuclear and plasma membranes, here termed the cell membrane (Fig. 2B). The general chromatin consists of electron dense filaments in a pale matrix, as in most brachyurans, but is less densely packed than in xanthids (see Discussion).

FIG. 4. *Mictyris longicarpus*, a mictyrid thoracotreme. A. Transmission electron micrograph of a longitudinal sagittal section of the spermatozoon. B. Transverse section to show the 'onion ring' lamellation of the acrosome. Abbreviations: ab = apical button of operculum; ba = branches of lateral arms; cl = concentric 'onion ring' lamellation; ia = inner acrosomal zone; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pe = vestigial periacrosomal cytoplasm; prml = microtubules of perforatorium; so = subopercular zone; tr = thickened ring; xrm = putative modification of xanthid ring



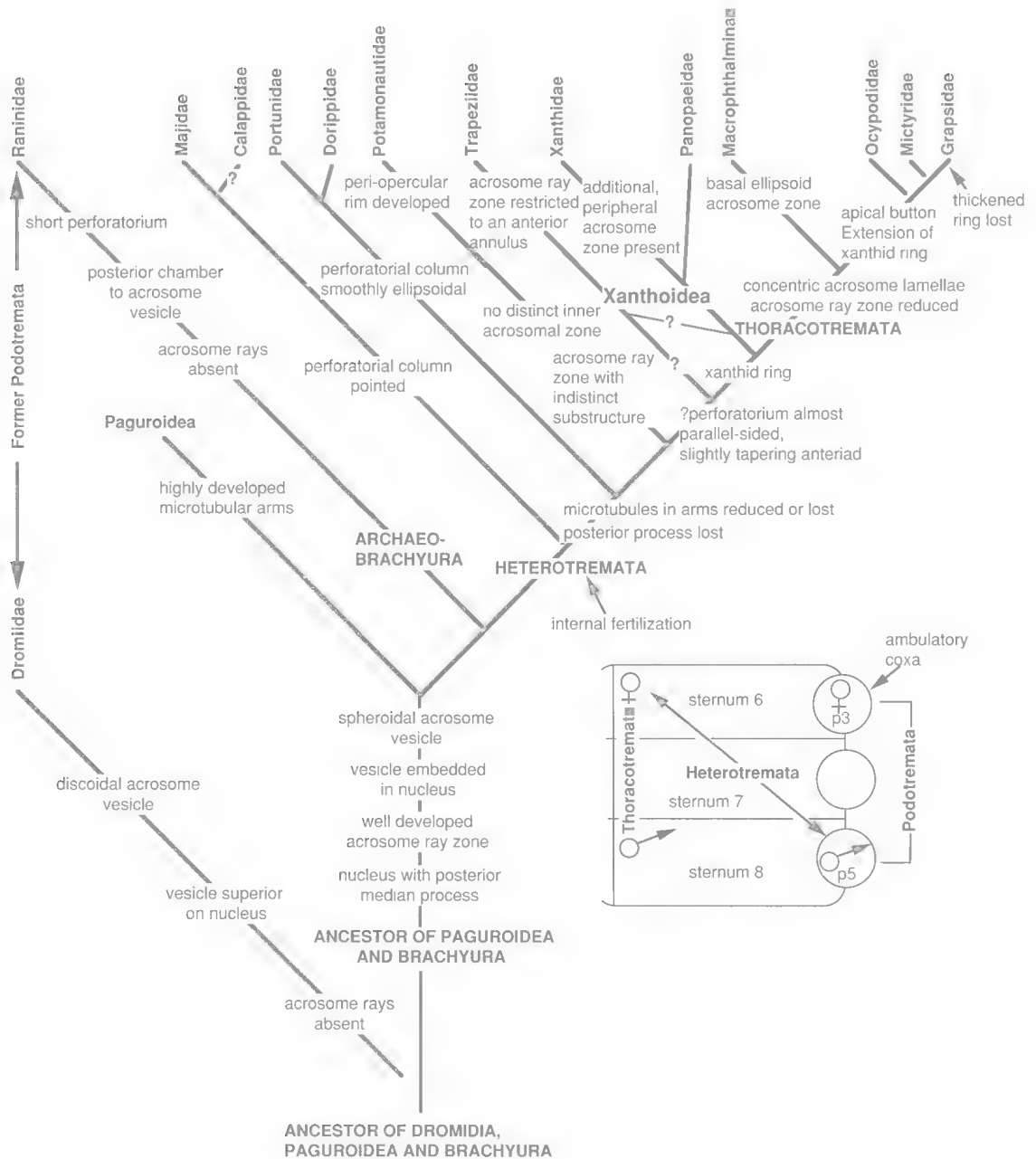


FIG. 5. Tentative phylogeny of the Brachyura based on apparent trends in the evolution of spermatozoal ultrastructure (modified from Jamieson, 1991). The chart of taxonomic features of location of gonopores is after Guinot (1978). The basal position of the Dromiidae, below the Paguroidea, which was tentatively suggested as an alternative to a brachyuran relationship by Jamieson (1991), is supported by evidence from rRNA (Spears et al., in preparation, cited in Abele, 1991). The position of the Potamonautidae is based on description of the sperm of *Potamonautes* by Jamieson (1993).

DISCUSSION

We may now consider the relationships of *Trapezia* as indicated by spermatozoal ultrastructure. These are tentatively indicated in Figure 5 within the context of a phylogeny of the Brachyura based on apparent trends in spermatozoal evolution.

The following are features of the spermatozoon of *Trapezia* that are general for heterotremes: extension of the subacrosomal chamber almost to anterior apex of the sperm whereas it reaches only to the approximate equator of the acrosome in the archaeobrachyuran *Ranina*; division of the acrosome contents into inner and outer zones; presence of an acrosomal ray zone at the periphery of the inner acrosomal zone; presence of a thickened ring where the capsule surrounds the base of the subacrosomal chamber; and absence of thoracotreme features mentioned below. A feature shared with 'higher' heterotremes is the restriction of cytoplasm to the periacrosomal region; unlike majids, for instance, it does not extend into the arms. The sperm of *Trapezia* thus confirms its heterotreme status and endorses separation from thoracotremes (Guinot, 1977, 1978) on the basis of the arrangement of the genital pores.

Features of the spermatozoon of *Trapezia* that are shared with the Xanthidae (compare Figs 2B & 3), at least as exemplified by investigated Xanthinae and Chlorodiinae, and the Panopeidae, exemplified by *Eurytium limosum*, include all of the above general heterotreme features but also the following apparently apomorphic xanthid features: the structure of the perforatorium, tapering anteriorly, with a fibrous core; and extension of the chromatin around the operculum, leaving only the raised central area of this exposed, the latter feature less developed in *Eurytium* than in the xanthids. These features are of questionable significance and could possibly arise homoplasially. Nevertheless, the form of the perforatorium is shared only with xanthids and *Eurytium* and, bearing in mind differences in sperm structure from the latter family outlined below, is not inconsistent with recognising relationship of *Trapezia* with xanthids though in a separate family.

Peculiar features of xanthids (Xanthinae, Chlorodiinae) (Jamieson, 1989a, and this study) and panopaeids (Jamieson & Abele, unpublished) which separate them from all other investigated heterotremes are the dense 'xanthid ring' around the base of the subacrosomal chamber and, in xanthids only, the additional peripheral zone out-

side the outer acrosomal zone (Fig. 3). A presumed derivative of the xanthid ring occurs in thoracotremes (see *Micruris*, Fig. 4A) and this fact suggests that the Xanthidae are an advanced heterotreme group near the base of the Thoracotremata (see Jamieson, 1991). Presence of the ring or its derivatives indicates that although the xanthids and such thoracotremes form a monophyletic group, the Xanthoidea, as it is currently understood, is a paraphyletic group. The absence of the ring in *Trapezia* may parsimoniously be taken to be plesiomorphic rather than due to loss because loss would involve one extra evolutionary step. This, with the xanthid-like perforatorium and undoubted somatic similarities of *Trapezia* and xanthids, suggests that *Trapezia* is the plesiomorphic sister-taxon or, at least a neighbouring taxon, of the xanthid-panopaeid assemblage in so far as they are represented spermatologically by xanthines, chlorodiines and panopaeids. In *Geryon* the ring is also absent (Jamieson, 1991, from micrographs by Hinsch, 1988). The condition in other xanthoids is unknown.

Whereas the sperm of *Trapezia* shows clear heterotreme features, it lacks thoracotreme features, well exemplified by *Micruris* (Fig. 4A,B), which include the perforate operculum with apical button (excepting *Macrophthalmus*); absence of the acrosome ray zone; absence of the thickened ring; and presence of concentric 'onion ring' lamellation of the outer acrosome zone (excepting *Uca*).

In conclusion, spermatologically *Trapezia* confirms its heterotreme position, shows features (especially the form of the perforatorium) linking it with xanthids and panopaeids, but warrants separate familial status in lacking the xanthid ring. It remains to be seen whether examination of sperm ultrastructure in further xanthoids will confirm this conclusion.

ACKNOWLEDGEMENTS

I am deeply grateful to Dr Danièle Guinot for providing information on the taxonomic status of *Trapezia*. I am also indebted to Miss Jenny Munoz for making some observations, Mrs L. Daddow, Mr C. Tudge and Mr D. Scheltinga for technical assistance, to Mr P. Davie and Mr J. Short for identifying *Trapezia coerulea*, and to Mr C. Tudge and an anonymous reviewer for constructive comments on the manuscript. The computer-generated line drawings are by the

author. This work was made possible by Australian Research Council funding.

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A TAXONOMIC REVISION OF THE EASTERN AUSTRALIAN EARTHWORM
GENUS *PERISSOGASTER* FLETCHER (MEGASCOLECIDAE: OLIGOCHAETA)

B.G.M. JAMIESON

Jamieson, B.G.M. 1993 06 30: A taxonomic revision of the eastern Australian earthworm genus *Perissogaster* Fletcher (Megascolecidae: Oligochaeta). *Memoirs of the Queensland Museum* 33(1): 235-244, Brisbane, ISSN 0079-8835.

The three species assigned to *Perissogaster* by Fletcher are redescribed. Of these *P. nemoralis* and *P. queenslandica* are shown to have on each side in caudal segments a median nephridium with preseptal funnel flanked by astomate meronephridia, all nephridia being exonephric. This dichogastrin condition of the nephridia, coupled with multiplication of gizzards, is considered to warrant placing the two species in the genus *Digaster* Perrier. The trigastric condition is verified for *P. nemoralis* but *P. queenslandica* is shown to have only two gizzards. It is demonstrated for the first time that *P. excavata*, the trigastric type species of *Perissogaster*, has at least 100, mostly preseptal, nephrostomes on each side per segment caudally, a condition attributable to the Tribe Megascolecini. It is nevertheless argued that this species is closely related to *Digaster*. Parsimony analysis is equivocal between origin of *P. excavata* within *Digaster* or a sister-group relationship to the *Digaster-Didymogaster* assemblage. The latter derivation is compatible with (though not necessitating) parallel development in *P. excavata* of multiple gizzards from a monogastric ancestor with or without multiple nephrostomes. A monotypic genus *Perissogaster* is redefined for *P. excavata*.
□ *Perissogaster*, *Digaster*, *Didymogaster*, nephridia, taxonomy, parsimony analysis.

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Perissogaster was erected by Fletcher (1887) for a new species, *P. excavata*, which differed from all known Australian oligochaetes in possessing three gizzards. Subsequently, Fletcher 1889, included *P. nemoralis* and *P. queenslandica* on the grounds that they also were trigastric.

Beddard (1895) placed *Perissogaster* and *Didymogaster* in *Digaster* because the three entities shared lobate prostates, meronephridia and more than one gizzard and were restricted to Australia. Michaelsen (1900) again separated the three genera but Sweet (1900) and Jamieson (1963) included the three species of *Perissogaster* in *Digaster* while excluding *Didymogaster*. Jamieson (1970, 1971) showed that *P. queenslandica* had dichogastrin nephridia (a stomate exonephric meronephridium median to astomate meronephridia on each side in caudal segments) and could therefore be retained in *Digaster* which has the same nephridial condition. It was, however, suggested that *P. excavata* and *P. nemoralis* should be excluded from *Digaster* in a reinstated *Perissogaster* as only astomate nephridia were demonstrated. *Perissogaster* was formally restricted to these two species by Jamieson (1975) but it was stated that the existing material of the genus was not in sufficiently good condition to allow full characterisation of the genus. The kind-

ness of Dr Courtenay Smithers in forwarding to the author a well preserved specimen which has proved to be *Perissogaster excavata* has allowed a reappraisal of the anatomy of this species revealing an unsuspected nephridial anatomy and has prompted redescription of the types of *P. nemoralis* and *P. queenslandica* which, again, are found to differ significantly from previous descriptions.

All figures are drawn by camera lucida. The following abbreviations are used in Figs 1&2: ♀, female pore; g.m. accessory genital marking; ♂, male pore; ♀ po, male porophore; pr.d, prostate duct; pr.g. glandular portion of prostate; sp. amp, spermathecal ampulla. sp. div, spermathecal diverticulum; sp.p, spermathecal pore; v.d, vas deferens. Roman numerals indicate respective segments. Registration numbers prefixed by AMW are housed in the Australian Museum.

TAXONOMY

Perissogaster Fletcher, 1887 emend.

Type species: *Perissogaster excavata* Fletcher, 1887.

DIAGNOSIS

Setae lumbricine. Gizzards 3, in V, VI and VII; extramural calciferous glands absent. Meri-

nephric; with numerous preseptal funnels on each side in each intestinal segment. Combined pores of a pair of tubuloracemose prostates and the vasa deferentia in XVIII. Spermathecae with pores at the anterior margins of their segments.

DETAILED DEFINITION

Setae 8 per segment; dorsal setal couple (*cd*) significantly wider than the ventral couple (*ab*). Clitellum anterior to the male pores. Combined male and prostatic pores a pair on XVIII. Accessory genital markings present. Female pores a minute pair presetally in XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9.

Some preclitellar septa very strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII, those in X-XII latero-oesophageal; preceding commissurals dorsoventral only; supra-oesophageal vessel oesophageal only; a pair of anterior lateroparietal trunks becoming latero-oesophageal and passing median to the dorsoventral commissurals to join the oesophageal plexus. Subneural vessel absent. Three oesophageal gizzards in V, VI and VII; extramural calciferous glands absent; intestine commencing in XVI, lacking muscular thickening, caeca and typhlosole.

Meronephric; enteronephric tufts in II-IV; astomate exonephric parietal micromeronephridia in succeeding segments but from XIV to the caudal extremity numerous preseptal nephrostomal funnels on each side in each segment; intestinal enteronephry not demonstrated. Holandric; gyniorchous; seminal vesicles in IX and XII. Prostates 1 pair, tubuloracemose. Fan shaped ovaries, and funnels, in XIII. Spermathecae short-stalked with small, sessile, lobed diverticulum.

DISTRIBUTION

New South Wales: Hawkesbury to Hunter River districts

REMARKS

The presence of multiple nephrostomes here demonstrated for *P. excavata* for the first time, sets *Perissogaster* apart from *Digaster*, no other described characters necessitate separation of the two genera.

Perissogaster excavata Fletcher, 1887
(Figs 1A, 2A, B)

Perissogaster excavata Fletcher, 1887: 383-387.

Digaster excavata; Beddard, 1895: 486; Sweet, 1900:

123. Buchanan, 1909: 73; Jamieson, 1963: 85-90; 1971: 75.

Perissogaster excavata; Fletcher 1889: 1528; Michaelsen, 1900: 193; 1907: 162; Bage, 1910: 231; Jamieson, 1970: 44; 1975: 268-269.

MATERIAL EXAMINED

'Tuglo' property, near Mt Royal, 48km north of Singleton, under a stone on very clayey muddy soil, collector C.N. Smithers, 8 February, 1976 - 1 clitellate specimen, AMW6644. Identification checked against a badly macerated much-dissected type specimen from Morpeth, AMW 1457.

DESCRIPTION

Length = 280mm, width (midclitellum) = 16mm, greatest width (forebody) = 18mm, 175 segments (69-334mm long, 3-15mm wide, 160-195 segments; Fletcher, 1887). Form circular in cross section. Segments II and III biannulate; remaining segments to XIV triannulate, IV weakly, the others strongly; thereafter with a strong postsetal furrow. Pigmented grey, excepting the pale ventrum, in alcohol. Prostomium proepilobous, short and broad, it and the peristomium with many longitudinal furrows. Dorsal pores absent (sometimes about 20 rudimentary pores posteriorly, Fletcher, 1889: 1528). Setae in 8 regular longitudinal rows throughout, commencing on II; minute but distinctly visible; setae *a* and *b* not visible in XVIII. In XII *aa:ab:bc:cd:dd* = 2.96:1.00:1.60: 1.50:2.68; circumference = 55mm; *dd:u* = 0.19. Nephropores not externally recognisable. Clitellum annular, XIV-XVII, with weak development to 1/2XIII and 1/2XVIII dorsally; (1/3XIII-part or most XVIII; Fletcher, 1887) intersegmental furrows and setae retained. Male pores (Fig. 1A), from internal examination, on small indistinct elliptical papillae equatorially in XVIII in *ab* (not visible externally; Fletcher, 1887). Accessory genital markings paired presetal eye-like markings in XVIII-XXII in *bc* and a transverse glandular trough similarly located in XXIII but continuous across the ventrum; the markings in XVIII also lying in a transverse elliptical trough which impinges on the posterior region of XVII; the troughs in XVIII and XXIII with numerous longitudinal stigmata; the accessory markings and male pores lying in a rectangular flattened and thickened area. (Accessory markings limited to XVIII-XXI; Fletcher, 1887). Female pores small but distinctly visible, a pair presetally and well median of *a* lines of XIV in a common whitish glandular area which interrupts the clitellum pre-

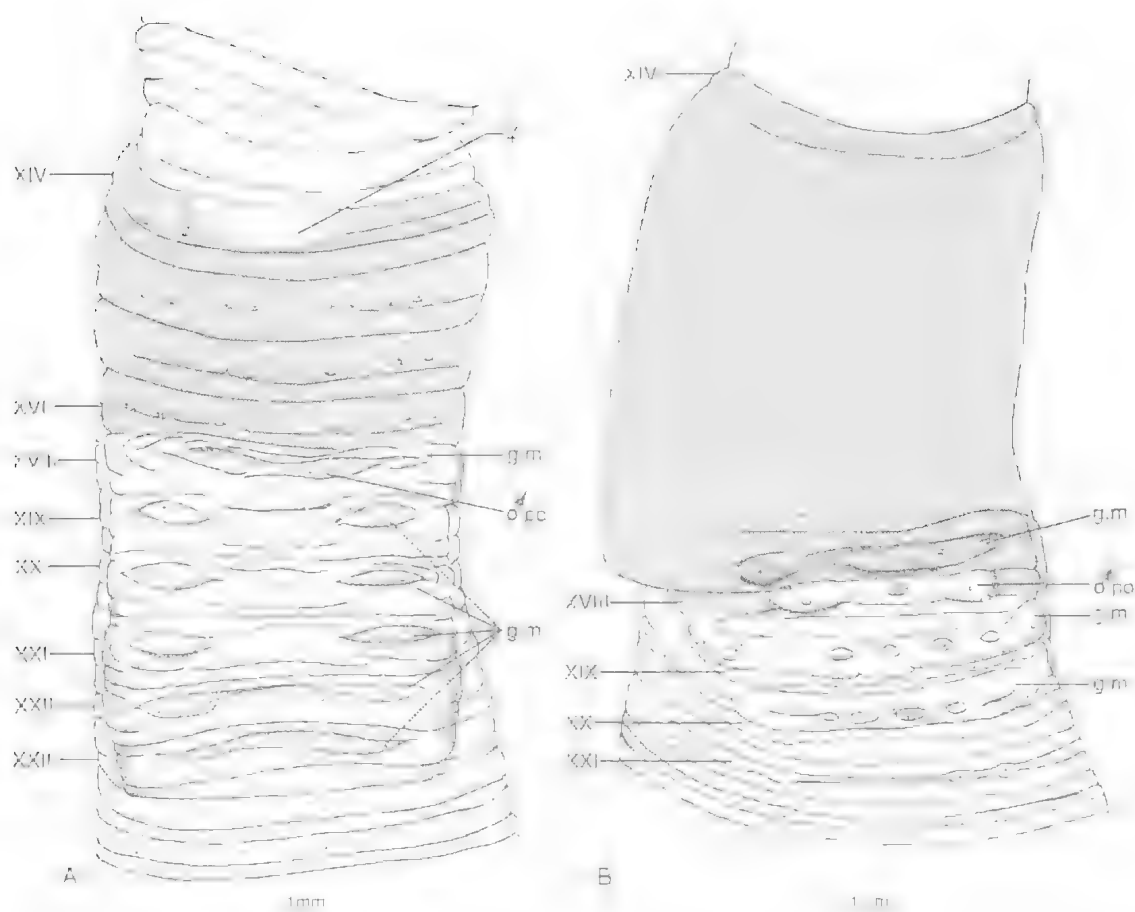
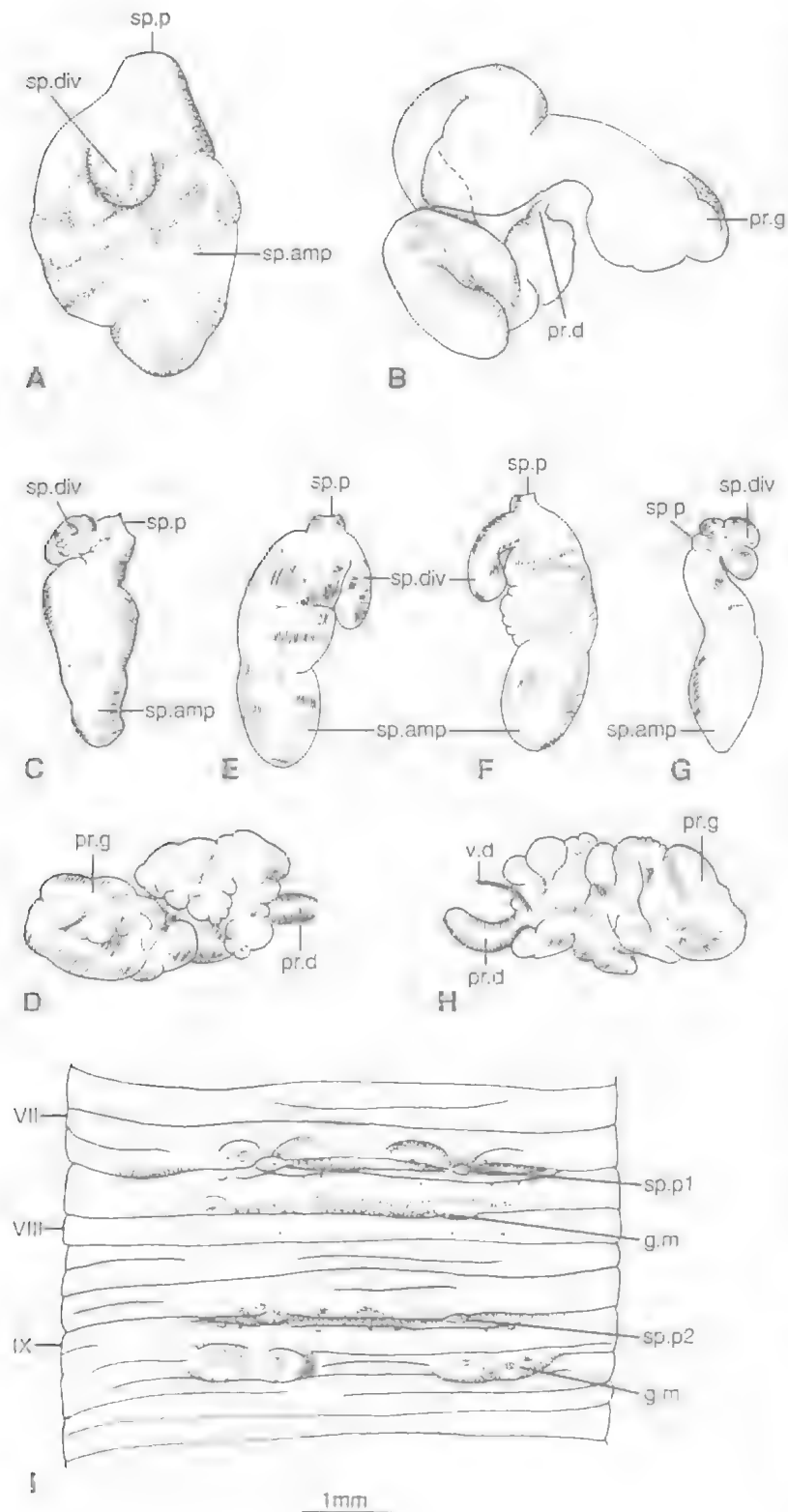


FIG. 1. Genital fields. A, *Perissogaster excavata* (TUGLO specimen); B, *Digaster nemoralis* (paralectotype). Clitellum shaded.

setally. Spermathecal pores not externally visible, in 7/8 and 8/9, appearing from internal examination to lie in *b* lines but stated by Fletcher (1887) to be in *a* lines.

Some preclitellar septa thickened; 9/10-12/13 (-13/14; Fletcher, 1887) immensely strong; tendons connecting the septa, of which those between septum 5/6 anteriorly are very strong. Dorsal blood vessel single, continuous onto the pharynx and passing under the brain. Last hearts in XII, those in X-XII large and latero-oesophageal, each receiving a broad short connective from the supra-oesophageal vessel and a longer slender connective from the dorsal vessel but otherwise unbranched; commissurals in V-IX (IV-IX; Buchanan, 1909) slender and dorsoventral only, though valvular, and each giving a lateral branch to the body wall before joining the ventral vessel. Supra-oesophageal from 3/4IX to XIII (VIII-

XIII; Buchanan, 1909), rudimentary in the last segment; adherent to the oesophagus. A large, free latero-oesophageal trunk present on each side, median to the dorsoventral commissurals in V-IX, ending in the plexus on the floor of the oesophagus in IX and continuous in IV anteriorly as a thick longitudinal ventrolateral parietal trunk. Subneural vessel absent. Oesophagus forming 3 large subspherical strongly muscular gizzards, in V, VI and VII, decreasing in size posteriad, each constricted off from but abutting on the others without appreciable intervention of unmodified oesophagus (connected by short pieces of oesophagus; Fletcher, 1887). The oesophagus simple, lacking calciferous glands, in VIII-XV, though internally with low papillae. Intestine commencing in XVI, muscular thickening, caeca and typhlosole absent. Nephridia micronephridia: tufts of numerous astomate micronephridia



on and lateral to the pharynx in II, III and IV send composite ducts to the pharynx in III and IV and those of II to the buccal cavity; numerous minute astomate exonephric parietal micromeronephridia in V-XIII, becoming very dense in XIV in which many are, in addition, adherent to the posterior septum; very numerous shortly stalked nephrostomes present on the anterior face of septum 14/15 and apparently arising mostly from the dense bands of exonephric septal nephridia on the posterior face of this septum. Nephridia in XV and succeeding segments dense bands on the anterior and posterior septa, with numerous funnels restricted to the anterior face of the posterior septum; parietal nephridia few but at least some of them with funnels. By XIX the nephridial bodies are chiefly on the posterior face of each septum, with more than 100 stalked funnels on the anterior face of the septum on each side; parietal nephridia are very few. In the caudal region nephridia are dense on the anterior faces of the septa, co-

FIG. 2. A, B, *Perissogaster excavata* (paralectotype): A, left spermatheca of IX; B, right prostate. C, D, *Digaster queenslandica* (lectotype): C, left spermatheca of IX; D, left prostate. E-I, *Digaster nemoralis*: E, F, ventral and dorsal views of left spermatheca of IX (lectotype); G, right spermatheca of IX (paralectotype); H, right prostate (paralectotype); I, spermathecal genital field (paralectotype).

existing with numerous stalked funnels and less numerous, with very few evident funnels, on the posterior faces, parietal nephridia are absent; no enteronephry is demonstrable.

Testes and large iridescent funnels in X and XI; testis-sacs absent; seminal vesicles racemose, much divided, in IX and XII, the posterior pair the larger. Prostates (Fig. 2B) tubuloracemose, restricted to an enlarged segment XVIII (or unilaterally in XVIII and XIX; Fletcher, 1887) each basically a broad tortuous tube but with some portions, particularly at the ental end, fused so that the tubular form has in places been lost; almost sessile, the short duct being concealed in the body wall (vas deferens opening into the duct at the base of the gland; Sweet, 1900). Fan-shaped ovaries, and funnels, in XIII. Spermathecae (Fig. 2A) 2 pairs, in VIII and IX, each virtually sessile on the body wall, with flattened ovoid ampulla and short broad diverticulum on its anterodorsal surface, the diverticulum more or less bi- or trilobed.

Digaster Perrier, 1872

D. nemoralis must now be added to the genus, as redefined by Jamieson (1975), as it is here shown to have the dichogastrin condition of the nephridia seen in all species of *Digaster*. The following changes in the definition are necessitated by the present study: *P. queenslandica* must be excluded from the statement that there may be 3 gizzards (see account below). This number is now limited in *Digaster* to *D. nemoralis* and variant individuals (Jamieson, 1963) of *D. perrieri*. The intestinal origin in the genus is now XVI-XIX and absence of a typhlosome is no longer constant as a typhlosome is present in *D. nemoralis*.

Digaster nemoralis (Fletcher, 1889) (Figs 1B, 2E-I)

Perissogaster nemoralis Fletcher, 1889: 1527-1528.

Digaster nemoralis; Beddard, 1895: 486; Jamieson, 1963: 86; 1971: 75.

Perissogaster nemoralis; Michaelsen, 1900: 198; Jamieson, 1970: 44; 1975: 268-269.

MATERIAL EXAMINED

Gosford, New South Wales, 2 clitellate, much dissected type specimens, AMW 1438, here designated the lectotype (L) and paralectotype (P).

DESCRIPTION

Length = 90+, 105mm, width (midclitellum) = 5.5mm, greatest width (forebody) = 6mm (lectotype, paralectotype), segments (P) 192. Form circular in cross section. Segments I-III simple; IV biannulate with the setae on the anterior annulus; from V, segments quadriannulate with the setae on the second annulus, and often with faint additional furrows; postclitellar segments triannulate. Pigmentless buff in alcohol. Prostomium broad, probolous or perhaps slightly proepilobous, it and the peristomium with many longitudinal furrows. Dorsal pores visible posteriorly, location anteriorly indeterminable owing to previous dissection (commencing after about X; Fletcher, 1889). Setae minute, in 8 regular longitudinal rows throughout, commencing on II; setae *a* and *b* replaced by penial setae in XVIII; in XII $aa:ab:bc:cd:dd = 3.25:1.00:3.30:1.94:13.09$; circumference = 15.4mm; $dd:u = 0.47$. Nephropores not externally recognisable. Clitellum annular, XIV-1/2XVIII; intersegmental furrows, dorsal pores and setae suppressed. Male pores in XVIII (Fig. 1B) on distinct ellipsoidal papillae, in *a* lines; the two papillae medianly conjoined by a transverse boss which widens medianly around a midventral oval pit-like glandular stigma. A median transverse pad present in each of intersegments 17/18, 18/19 and 19/20, each with a transverse series of similar stigmata. Numerous stigmata associated with tumescence (Fig. 2I) also present in VII, VIII and IX in association with the spermathecal pores. Female pores not visible. Spermathecal pores on distinct papillae in 7/8 and 8/9, in *a* lines.

Some preclitellar septa thickened: 5/6-9/10 very strong. Dorsal blood vessel single, anterior course indeterminable owing to previous dissection. Last hearts in XIII; those in X-XIII large and latero-oesophageal, each receiving a broad short connective from the supraoesophageal vessel and a longer slender connective from the dorsal vessel but otherwise unbranched; commissurals in VIII (and IX?; and further anteriorly?) slender and dorsoventral only and each giving a lateral branch to the body wall before joining the ventral vessel. Supraoesophageal vessel narrow and adherent to the oesophagus but limits indeterminable. Broken latero-oesophageal trunks observed in segment VI. Subneural vessel absent. Oesophagus forming 3 large strongly muscular gizzards, in V, VI and VII, each bowl-shaped and occupying the posterior half of the segment, the oesophagus in the anterior half being similarly dilated but only slightly muscularised. Oesophagus very short,

almost suppressed, in VIII; in IX and X short but laterally expanded and in XI-XIV forming paired, very conspicuous, strongly vascularised dilatations, increasing in size posteriorly to very large in XIV; these dilatations dorsolateral, internally with numerous low lamellae but not constricted off from the general oesophageal lumen. Oesophagus in XV and XVI narrow but invaginated into the dilatation in XIV in which it has the appearance of a rosette-like valve. Intestine commencing, with abrupt widening, in XVI; muscular thickening and caeca absent; a deep laminar dorsal typhlosole present. Nephridia meronephridia; large astomate tufts with many spiral loops in II-IV send a common (multiple?) duct forward on each side, traced anteriorly in II but further course indeterminable. Smaller aggregates with lateral outliers in V to VII are restricted to the posterior septum but are exonephric by separate individual ducts, one from each nephridium. By VIII the nephridia form a transverse exonephric band of several moderately large meronephridia at junction of posterior septum and body wall. By XII the band of several nephridia on each side is parietal with the forwardly directed ducts entering the body wall presegmentally; from XIII there is an increasing tendency for the median nephridia to form diffuse aggregations, though by about XXII these aggregations have reduced to 2 to 3 nephridia lateral to which are 4 smaller nephridia forming regular longitudinal rows; all nephridia are exonephric, avascular and apparently astomate. Towards the caudal end there are 3 well spaced nephridia on each side in very straight longitudinal rows lateral to what appear to be two or more aggregated nephridia. In the paralectotype which, unlike the lectotype, is complete posteriorly, the median-most nephridium in several posterior segments has a presegmental funnel and is enlarged as an exonephric megameronephridium. Finally in approximately 7 most posterior segments the regular arrangement of nephridia breaks down, nephridial loops filling the segments transversely and the median nephridium is further enlarged; the lateral nephridia appear to be interconnected by a medianly directed duct; the median nephridium retains the presegmental funnel but whether it and the lateral nephridia are exonephric or enteronephric is indeterminable. Testes and large iridescent sperm funnels in X and XI; testis-sacs absent; seminal vesicles racemose, large, in IX, XI and XII. Prostates (Fig. 2H) racemose: subrectangular deeply incised lobes, with stout moderately long muscular duct which branches within the gland and entally re-

ceives the vas deferens. Perianal setae slender entally strongly curved needles, the ectal tip delicately pointed with recurved extremity; ectal region with a few fine apically directed spines; a mature seta (paralectotype) 0.96mm long; the shaft 21 μ m wide at midlength. Bushy ovaries and funnels, in XIII; ovisacs not recognisable. Spermathecae (Fig. 2E,F,G) 2 pairs, in VIII and IX, each with elongate sacciform to pointed ovoid ampulla which is joined ectally and anteriolaterally by a clavate inseminated diverticulum, duct ectal to the ampulla very short. In the paralectotype the diverticulum is bi- or usually multi-loculate.

Digaster queenslandica (Fletcher, 1889)
(Fig. 2C,D)

Perissogaster queenslandica Fletcher, 1889: 1529-1530

Digaster queenslandica; Beddard, 1895: 485; Sweet, 1900: 124; Jamieson, 1970: 44; 1971: 75; 1975: 268-269.

Perissogaster queenslandica; Michaelsen, 1900: 199; 1916: 22-24.

MATERIAL EXAMINED

Oxley, southeast Queensland, collector T.G. Sloane, AMW1408, two specimens here designated lectotype (L) and paralectotype (P).

DESCRIPTION

Length = 162mm, width at segment XV = 6.5mm, greatest width (forebody) = 8mm, segments 215. Form circular in cross section but with some ventral flattening posteriorly. Segments I to III simple; from IV biannulate with setae on the posterior annulus and sometimes with weaker further annulation; simple from approximately XX posteriorly. Pigmentless buff in alcohol. Prostomium prolobous though longitudinal furrowing of the peristomium perhaps includes a narrow dorsal tongue. Dorsal pores unusually obvious, first in 4/5 but with a rudiment in 3/4. Setae in 8 regular longitudinal rows throughout, *a* and *b* absent in XVIII; in XII, *aa:ab:bc:cd:dd* = 2.57:1.00:2.00:1.78:18.57; circumference = 21.5mm; *dd:u* = 0.60. Nephropores not externally recognisable. Clitellum not developed. Male pores in XVIII, in *a* lines, on small almost contiguous papillae. Female pore unpaired in XIV, midway between the setal arc and anterior margin. Spermathecal pores 2 pairs, minute but distinctly visible in VIII and IX, appreciably be-

hind the anterior margin; those in IX 0.55mm apart.

Septa 4/5 and 5/6 fairly strongly thickened; 6/7 and 7/8 slightly thickened; 8/9 moderately strongly; 9/10-13/14 strongly thickened, 11/12-13/14 especially so. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII; those in X-XII large and latero-oesophageal, each receiving a broad short connective from the supra-oesophageal vessel and a slender connective from the dorsal vessel but otherwise unbranched; commissurals in (V?) VI-IX slender and dorsoventral only and each giving a lateral branch to the body wall before joining the ventral vessel. Supra-oesophageal vessel well developed in X-XII, weakly developed in IX and 1/2XIII. A large latero-oesophageal trunk on each side median to the commissurals joining the supra-oesophageal vessel in X and traceable forward at least to VI. Subneural blood vessel absent. Oesophagus with only 2 gizzards (contrary to Fletcher, 1889), in VI and VII, each very large, strongly muscular and subcylindrical, abutting on each other with almost inappreciable intervening oesophagus; that in VI preceded in the anterior portion of the segment by unthickened oesophagus. The oesophagus in V dilated to almost the size of a gizzard but its musculature unthickened, a spurious impression of a gizzard being produced by the ensheathing muscular septum 5/6. Dilatation and vascularisation of the oesophagus in XIV-XVI but no calciferous glands. Intestine commencing in XVIII; muscular thickening absent; caeca and typhlosolae not recognisable but maceration precludes certainty. Nephridia all avesciculate meronephridia: dense aggregations of meronephridial tubules on the parietes in II-IV appear exonephric but tubules adherent to the pharynx are possibly enteronephric; from V to the anterior intestinal region astomate, avesciculate micromeronephridia scattered on the parietes, the nephridia decreasing in size and becoming more numerous (many) posteriorly; never forming regular longitudinal rows. Caudally, in the last approximately 18 segments, with 15-20 astomate parietal micromeronephridia in transverse single file on each side lateral to an exonephric(?) megameronephridium with large preseptal funnel. Testes and funnels in X and XI, funnels in XI larger and iridescent; seminal vesicles large, racemose, in XI and XII. Prostates (Fig. 2D) depressed elongate tongue-shaped, sufficiently incised to be considered racemose but with a main, central canal from which many lesser side branches supply the lobes; ectal duct short,

weakly muscular and largely concealed in loose parietal musculature. Penial setae absent. Ovaries presumably represented by a pair of large depressed lobes with no evident oocytes on the anterior septum of XIII; funnels on the posterior septum. Spermathecae (Fig. 2C) 2 pairs, in VIII-IX, each with conical-ovoid ampulla and short, wide duct; which is joined anterolaterally by a compact inseminated internally multiloculate and externally slightly lobed diverticulum.

REMARKS

The demonstration above that Fletcher and Michaelsen were incorrect in recognising a third gizzard in this species gives unexpected support to the author's contention (Jamieson, 1970) that the previously described anatomy and the hitherto unrecognised dichogastrin condition of the nephridia warranted placing it in *Digaster*.

Michaelsen (1916) recorded this species from Brisbane, southeast Queensland.

CLADISTICS

As an adjunct to taxonomic considerations of the status of *Perissogaster* the relationships of the three species formerly placed in the genus to each other and to *Digaster* and *Didymogaster* have been investigated, using the PAUP program of Swofford (1990), version 3.0s, using 30 characters for 25 species (Jamieson, unpublished). Suffice to say the exhaustive and branch-and-bound search options gave a very large number of trees with grossly discordant topologies and that a consensus tree gave no resolution beyond separating the two *Didymogaster* species as the sister-group of the *Digaster*-*Perissogaster* assemblage. This assemblage formed a single polytomy. Many of the characters proved highly homoplastic.

A subset of 15 of the less noisy characters applied to only 11 taxa, consisting of a hypothetical ancestor (hypanc), the three *Perissogaster* species, the two *Didymogaster* species, and representatives of the *lumbricoides* and *perrieri* groups within *Digaster* (details below) produced a single tree (Fig. 3) in a branch-and-bound search. In view of the discordant results when the full character-taxon set is used, or when additional taxa are added to the reduced set, this single tree can be regarded as only one of many objective hypotheses of relationships. It is possible that the true phylogeny is not recoverable from the morphology of extant species of the total assemblage. The single tree obtained will, nevertheless be used in the following 'intuitive' discussion of

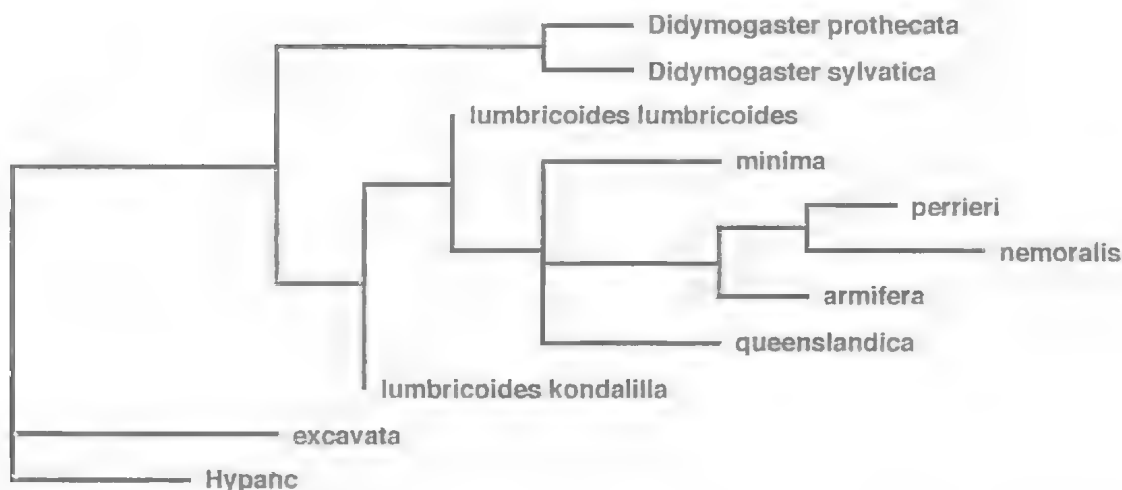


FIG. 3. Single tree obtained for 11 taxa indicated, and 15 characters, using the branch-and-bound option of the PAUP program. Tree length = 27. Consistency index (CI) = 0.778. Homoplasy index (HI) = 0.222. CI excluding uninformative characters = 0.667. HI excluding uninformative characters = 0.333. Retention index (RI) = 0.684. Rescaled consistency index (RC) = 0.532

relationships and in support of the taxonomic decision made.

An ancestor (hypanc) with a single gizzard and other characters indicated in the matrix was envisaged. Recourse, alternatively, to using the more objective out-group strategy, using *Didymogaster* as the outgroup, gave similar results.

CHARACTERS EMPLOYED

This list is a subset of those used in the more comprehensive analysis. As a result some of the characters (marked #) are uninformative or invariable. *Numbers are deducted from the states of some characters to limit their values to less than 10 and avoid hexadecimal notation.

- #1. Male pore(s) unpaired 1; paired 2.
2. Female pore(s) unpaired 1, paired 2.
- #3. Spermathecal pore(s) unpaired 1, paired 2.
4. First spermathecal segment.
5. Spermathecal pores, number of transverse sets.
6. Segment (-10) of last hearts.*
7. First gizzard segment.
8. Number of gizzards.
9. Caudal preseptal funnels 1, many 2.
10. Testes in X 1, X and XI 2, XI 3.
11. Seminal vesicles in IX, X, XI and XII 1, IX and XII 2, XI and XII 3, XII 4, IX, XI and XII 5.
12. Prostates tubular 1, tubuloracemose 2, racemose 3, racemose- bipartite 4.
13. Penial setae absent, 0 present 1.

- #14. Number of diverticula per spermatheca.
15. Diverticula uniloculate 1, multiloculate 2.

INPUT DATA

Taxon	123456789012345
<i>Didymogaster prothecata</i>	222643621224011
<i>Didymogaster sylvatica</i>	222733621224011
<i>Digaster lumbricoides</i>	
<i>lumbricoides</i>	22282262?233011
<i>kondalilla</i>	22282262?234011
<i>minima</i>	22282262?2343012
<i>perrieri</i>	2?282352?233111
<i>queenslandica</i>	212822621232012
<i>nemoralis</i>	2?2823531253112
<i>armifera</i>	22282252?223112
<i>Perissogaster excavata</i>	222822532222011
<i>Hypanc</i>	2225525112?1?11

BRANCH-AND-BOUND SEARCH SETTINGS

Initial upper bound: unknown (compute via stepwise).
 Addition sequence: furthest.
 Initial MAXTREES setting = 100.
 Branches having maximum length zero collapsed to yield polytomies.
 Topological constraints not enforced.
 Trees are unrooted.
 Multi-state taxa interpreted as uncertainty.
 Outgroup = *Hypanc*.
 Characters were all scored as unordered and unweighted.

DISCUSSION

From 'intuitive' taxonomic considerations, *Perissogaster nemoralis* and *P. queenslandica* are here included in *Digaster* because of the correlation of three points: general anatomy, multiplication of gizzards and dichogastrin nephridia. The dichogastrin nephridial condition occurs in earthworm genera of several zoogeographical regions of the world and has been accompanied by multiplication of the gizzard, from the usual monogastric condition, independently in the various regions. It has been argued (Jamieson, 1975) that the di- or trigastric condition in Australian earthworms originated in what is now the montane coastal province of the Eastern Sub-region, to which such forms are restricted, independently of evolution of this condition in other, non-Australian zoogeographic regions.

Multiplication of gizzards might have developed only once (strict monophyly) or in more than one lineage predisposed to this development by virtue of genetic similarity and relationship (parallelism or homoplasy). It is unlikely that a third hypothesis, development of the multigastric condition independently in unrelated taxa, is tenable as this would presuppose edaphic or other environmental factors favouring repeated development of the condition in the montane coastal province but absent from other provinces.

The taxa with multiple gizzards are (1) a large group of species, containing the type species, *D. lumbricoides* with two gizzards, in VI and VII, which is restricted to Queensland and northern New South Wales; (2) *D. perrieri* and *D. armifera*, with two gizzards, in V and VI, allopatric in New South Wales; (3) two species, comprising the genus *Didymogaster*, with the *lumbricoides* location of the gizzards, sympatric with *D. perrieri* and *D. armifera* in central New South Wales; and (4) the three species of *Perissogaster* s.lat., *P. excavata*, *P. nemoralis* and *P. queenslandica*.

With regard to the phylogenetic validity of these four groupings: on the basis of gizzard location the *lumbricoides* group might reasonably be assumed to form a monophyletic group. However, neither the restricted PAUP analysis (Fig. 3) nor analysis of the full taxon-character set supported monophyly.

Digaster perrieri and *Digaster armifera*, though sympatric with *Didymogaster*, differ from other *Digasters* and from *Didymogaster* in having gizzards in V and VI, and might be considered the sister-group of the *lumbricoides*-*Didymogaster* group. However, PAUP analyses do not sup-

port a monophyletic *perrieri*-*armifera* assemblage (Fig. 3).

Didymogaster has various conflicting positions in the PAUP analyses, including that of sister-group to *Digaster*, as shown in Fig. 3. Synapomorphies defining *Didymogaster* include intrasegmental location of spermathecal pores and presence of testis-sacs (neither character used in the restricted analysis). Its generic status is accepted here.

The relationship of the three former *Perissogaster* species may now be further considered. It has been shown that *Perissogaster queenslandica* is digastric, contrary to previous descriptions, with the *lumbricoides* location of the gizzards, in VI and VII and is placeable in *Digaster*, as supported in Fig. 3 and advocated by Jamieson (1970, 1971). *P. nemoralis*, sympatric with *D. armifera* and *D. perrieri*, is here transferred to *Digaster* as its only trigastric species (excepting variant individuals of *D. perrieri*). Consideration has been given to the possibility that the *armifera*-*perrieri* condition (gizzards in V and VI) and *lumbricoides* condition (gizzards in VI and VII or their homeotic equivalent) have developed dichotomously from the trigastric condition seen in *nemoralis*. It has been shown above that cladistic analysis does not support recognition of either group. Conversely, the trigastric condition might be considered to reflect a further development of the propensity in *Digaster* to thicken the oesophageal musculature in two of segments V to VII. The PAUP analyses support the latter view, presenting the trigastric condition as an apomorphy of *nemoralis* developed from the digastric condition of an ancestral *Digaster* perhaps (Fig. 3) shared with *D. perrieri*.

The relationships of the type species of *Perissogaster*, *P. excavata*, are especially uncertain. If multiple gizzards are evidence of relationship, it would appear that multiplication of nephrostomes characteristic of *P. excavata*, which would formerly have assigned it to the tribe Megascolecini sensu Jamieson (1971), has occurred in this species independently of acquisition of this condition in other genera of the tribe. This would support the author's contention that the Megascolecini may represent a grade rather than a clade. The anatomy of *P. excavata* is close to that of *P. nemoralis*, excepting the nephridial condition, extending to the origin of the intestine in XVI, unknown elsewhere in *Digaster*. However, an intuitive postulate of a sister-group relationship of *excavata* to the *Digaster*-*Didymogaster* assemblage is supported by the restricted PAUP

analysis (Fig. 3). It is equivocal as to whether the common ancestor of *excavata* and this assemblage had two or three gizzards despite indicating independent origin of three gizzards in *nemoralis* from the digastric condition. The common ancestor of *excavata* and the *Digaster-Didymogaster* assemblage is computed to have had the dichogastric condition of nephridia (single preseptal funnel on each side), retained as a plesiomorphy in *Digaster* but changing to the multifunnelled condition in *excavata*. Some trees from the larger data set nevertheless do associate *excavata* and *nemoralis* as sister-species within the *Digaster* assemblage.

The PAUP analyses are not sufficiently extensive to rule out the alternative possibility that *Perissogaster excavata* is descended from a monogastric megascolecine ancestor with its nephridial condition of multiple preseptal nephrostomes in caudal segments, conditions seen in *Oreoscolex* Jamieson. Two *Oreoscolex* species from New South Wales, *O. illawarrae* (Fletcher, 1889) and *O. saccurius* (Fletcher, 1886) agree with *P. excavata* in having the intestinal origin in XVI. However, confinement of multiplication of gizzards to a single zoogeographical province favours the view that multiplication is a rare apomorphy more likely to occur in closely related forms than in forms as distinct as *Oreoscolex*.

In view of the logical and computational ambivalence as to the position of *P. excavata* it is here considered that taxonomic convenience is best served by retaining this species in the monotypic genus *Perissogaster*. This has been redefined in the taxonomic section.

ACKNOWLEDGEMENTS

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ON THE ALLEGED OCCURRENCE OF THE EARLY CRETACEOUS AMMONITE *SIMBIRSKITES* IN QUEENSLAND

SIMON R.A. KELLY

Kelly, S.R.A. 1993 06 30: On the alleged occurrence of the Early Cretaceous ammonite *Simbirskites* in Queensland. *Memoirs of the Queensland Museum* 33(1): 245-251. Brisbane. ISSN 0079-8835.

The two ammonite specimens that comprise the Australian records of the Early Cretaceous genus *Simbirskites* are reassessed. Formerly described as *S. morvenae* Whitehouse, they are re-identified here as Late Jurassic, *Galbanites galbanus* Buckman and *G. fasciger* Buckman. The Australian specimens were supposedly from Queensland, but are believed here to be exotic, brought from England probably in the late nineteenth century. Their limestone lithology contrasts with the local clastic sediments. They closely resemble the form and lithology of specimens from the Portland Stone of England. Furthermore they are associated with gastropods, *Leptomaria rugata* (Benett), and bivalves including *Laevitrigonia damoniana* (de Loriol) and oysters which are also comparable to Portland Stone forms. Simbirskitids are typically boreal in their distribution, occurring in mid-Hauterivian to Early Barremian deposits in northern Europe, parts of the USSR and North America. Most other austral occurrences have been previously discounted. The geographically isolated Australian occurrence now should be deleted from the record. □ Late Jurassic, Early Cretaceous, ammonite, bivalve, gastropod, Portland Stone, *Simbirskites*, *Galbanites*, England, Queensland, Australia.

Simon R.A. Kelly, British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Rd, Cambridge CB3 0ET, England; 21 August, 1992.

In the Queensland Museum type collection, I recognised a moderately large, English, Portland Stone ammonite in characteristic limestone preservation. On reading the label, I was surprised to discover that this was reputedly from the Queensland Early Cretaceous. A smaller ammonite and three large gastropod internal moulds have been artificially attached with cement to the umbilicus. The two ammonites were placed in *Simbirskites* (Whitehouse, 1926) without sighting the specimens (Bryan & Whitehouse, 1926). Whitehouse (1927) described the smaller, Queensland Museum (QM) F16438, as type of *S. morvenae* sp. nov.; the larger (QM F1270) was made paratype. The ammonites are re-identified here, the larger one as *Galbanites* (*Galbanites*) *galbanus* (Buckman), and the smaller one as *G. (G.) fasciger* (Buckman). The gastropods (QM F21078-21081) originally determined as *Leptomaria* (?) (Etheridge, 1909) are identified here as '*Leptomaria*' *rugata* (Benett). In the matrix, Whitehouse (1927) identified fragments of '*Ostrea*' and '*Trigonia*'. The oyster may be *Liostrea* sp.; other undetermined oysters, possibly exogyrids, grew on the interior of the body chamber of the larger ammonite shell. The trigoniid shows an early commarginal ribbed phase, followed by later somewhat irregular tuberculation typical of *Laevitrigonia damoniana* (De Loriol, 1875).

'*Leptomaria*' *rugata*, *Liostrea*, exogyrids and *L. damoniana* are present in the English Portland Stone; the last is restricted to it and French stratigraphic equivalents. Stratigraphically, the youngest occurrences of *Laevitrigonia* s.s. are undescribed specimens in the Berriasian of the Russian Platform, and close to the Jurassic-Cretaceous boundary in the Cinder Beds of southern England (Kelly, 1988). It is unknown in the Hauterivian. However, it is well known in the Late Jurassic of northern and western Europe, and is particularly common in the Portlandian/Tithonian Portland Limestones of southern England.

The composite specimen was originally acquired from a Mr Hurst or Mr Hunter (Rozefelds et al., 1990) and was catalogued in the Queensland Museum as D7710.12 in 1893. The cited locality is 'Victoria Downs, Morven' where extensive outcrops of the marine, Aptian, Roma Series, are placed in the Doncaster Member of the Wallumbilla Formation (Exon, 1971). However, despite detailed geological survey work in the area, no further *Simbirskites*, nor specimens of similar lithology have been collected (Day, 1969: 152).

Etheridge (1909) originally compared the ammonites to *Perisphinctes kayseri* Neumayr & Uhlig (1881), now recognised as *Simbirskites*, which occurs in the *seeleyi* zone, Hauterivian, of north

Germany (Rawson, 1971). Whitehouse (1926, 1927) initially appeared to accept a Queensland provenance. Whitehouse (1946: 3) intimated that the ammonites were exotic, stating 'a little uneasiness is felt about the locality record' and that preservation of the specimens was like that of *simbirskitids* of north Germany which last remark is not supported here. Whitehouse (1954: 9 footnote) reiterated his belief of an extra Australian provenance. This remark was supported by Day (1969: 152). Lithologies of the large German *simbirskitids* figured by Neumayr & Uhlig are ironstones (Rawson, 1971), whereas most other German occurrences are from paralic sandstones or offshore clay facies. Sediments of the Wallumbilla Formation are predominantly sandstones with minor mudstones, but the specimens, supposedly from Morven, are preserved as internal moulds in a pale creamy brown limestone with much bioclastic debris. The preservation exactly matches that of parts of the English Portland Stone.

The *Simbirskitinae* is a boreal group of *Olcostephanidae*, one of the youngest in the once widespread *Perisphinctoidea*. It is characteristic of the mid-Hauterivian to earliest Barremian of northern England, northern Europe, the Russian Platform, Spitsbergen and North America (Rawson, 1971). Possible Late Valanginian forerunners occur in Arctic Canada (Jeletzky & Kemper, 1988).

The Australian record of *Simbirskites*, discounted here, has been widely quoted, (Wright in Moore, 1957). Other records of *simbirskitids* outside the normal geographical range for the group were reviewed by Rawson (1971). Mexican (Burckhardt, 1912) and Himalayan forms (Uhlig, 1910, were re-identified (*Grayiceras*) (Spath, 1924). Leanza (1958) described four species of *Simbirskites* from Argentina, but these appear to be *Rogersites*. Kilian & Piroulet (1905) recorded *Simbirskites* from New Caledonia, but the record remains unsubstantiated (Whitehouse, 1926).

SYSTEMATICS

Class CEPHALOPODA

Superfamily PERISPINCTOIDEA

Steinmann, 1890

Family PERISPINCTIDAE Steinmann, 1890

Subfamily DORSOPLANITINAE Arkell, 1950

Galbanites Buckman, 1922

Type species. Galbanites galbanus Buckman,

1922, Portland Stone, Haddenham, Buckinghamshire, England.

REMARKS

Arkell (in Moore, 1957) synonymized *Galbanites* and *Titanites* Buckman, 1921 but Wimbledon & Cope (1978) recognised *Galbanites* as distinct. The specimens described below as *Galbanites* have predominantly biplicate to triplicate ribbing, but lack the coarseness of the primaries which characterises *Galbanites* (*Kerberites*). The genus is widespread in the *okusensis* and *kerberus* Zones of southern England.

Galbanites (*Galbanites*) *galbanus*

Buckman, 1922 (Figs 1,2A,3)

1909 *Perisphinctes kayseri* Neumayr & Uhlig; Etheridge, p.239, pl.68 [larger specimen only; non Neumayr & Uhlig, 1881].

1922 *Galbanites galbanus* Buckman, pl.355, figs A,B,C.

1926 *Simbirskites* spp. Whitehouse, p.200 [larger specimen only].

1927 *Simbirskites morvenae* sp.nov. Whitehouse, p.111, paratype only [non pl.16, fig. 1; non text fig. 5].

1938 *Galbanites galbanus* Buckman; Roman, p.297.

1946 *Simbirskites*; Whitehouse, p.8.

1972 *Galbanites galbanus* Buckman; Clark, p.82.

1974 *Galbanites galbanus* Buckman; Wimbledon, p.146, pl. 18.

1978 *Galbanites galbanus* Buckman; Wimbledon & Cope, p. 184.

1990 *Simbirskites morvenae* Whitehouse; Rozefelds et al, p.701.

MATERIAL EXAMINED

HOLOTYPE: British Geological Survey, GSM47155, Haddenham Micritic Member (Blue and Cream Bed, Creamy Limestone), Portland Stone, works north of the railway station, Haddenham, Buckinghamshire, England (Buckman, 1922)

OTHER MATERIAL: QM F1270, originally catalogued as D7710.12 in 1893 and stated to be from Victoria Downs, Morven, Queensland. Donated by Mr Hurst or Mr Hunter. The provenance is believed here to be from the English Portland Stone.

DIAGNOSIS

Evolute perisphinctid with coarse biplicate to triplicate ribbing, branching just below mid-flank (Fig. 1). Whorl section rounded (Fig. 2A). Ribbing gently arched forward to rectiradiate, with only weak forward swing over the venter. Shell



FIG. 1. *Galbanites (Galbanites) galbanus* Buckman, 1922. Lateral view of internal mould of QM F1270 (largest specimen), showing QM F16438 (smaller specimen, *G. (G.) fasciger* Buckman) artificially attached to the umbilicus, together with four internal moulds of gastropods, QM F21078-21081, '*Leptomaria*' *rugata* (Benett), $\times 0.5$. (See also Figs 2,3 for further detail).

septate up to a diameter of 330mm. Body chamber outer two thirds whorl; aperture not seen; suture in Fig. 3. Maximum diameter 365mm; septate diameter 244mm; maximum whorl height 112mm, width 85mm; no. of ribs 55 primary, 133 ± 2 secondary.

REMARKS

The holotype of *Simbirskites morvenae* Whitehouse differs from the holotype of *Galbanites galbanus* Buckman by its larger size, and tendency towards triplicate as well as biplicate secondary ribs. It differs from *G. fasciger* by having rounded flanks, as opposed to flat sided, and the absence of fasciculation. *G. galbanus* occurs in the later *okusensis* and early to middle *kerberus*

zones of southern England (Wimbledon & Cope, 1978).

***Galbanites (Galbanites) fasciger* Buckman, 1923** (Fig. 1, centre; Fig. 2, B,C,D)

1909 *Perisphinctes kayseri* Neumayr & Uhlig; Etheridge, 239, pl.68 [small specimen only; non Neumayr & Uhlig, 1881].

1923 *Galbanites fasciger* nov. Buckman, pl.451.

1926 *Simbirskites* spp. Whitehouse, p.200 [small specimen only].

1927 *Simbirskites morvenae* sp.nov. Whitehouse, p.111, pl.16, fig. 1; text fig. 5 only.

1946 *Simbirskites*; Whitehouse, p.8.

1972 *Galbanites fasciger* Buckman; Clark, p.82.



FIG. 2. A, *Galbanites (Galbanites) galbanus* Buckman, 1922, ventral aspect of QM F1270, $\times 0.5$; B-D, *Galbanites (Galbanites) fasciger* Buckman, 1924; B, left lateral view, QM F16438, $\times 1$. (Holotype of *Simbirskites morvenae* Whitehouse, 1926); C, right lateral view of QM F16438, $\times 1$; D, ventral view of QM F16438, $\times 1$.

1974 *Galbanites fasciger*, Buckman; Wimbledon, p.72.

1990 *Simbirskites morvenae* Whitehouse; Rozefelds et. al, p.701.

MATERIAL EXAMINED

HOLOTYPE: British Geological Survey, GSM37302, formerly S. Buckman Collection 295556, purchased 1924, 'Lower Witchett', Creamy Limestone, Portland Beds, Barrel Hill, Long Crendon, Buckinghamshire, England.

OTHER MATERIAL: QM F16438, cemented to umbilicus of QM F1270, information as for *G. galbanus* above.

DIAGNOSIS

Moderately involute perisphinctid (Fig. 2 B,C), with flattened, ventrally converging sides (Fig. 2D). Ribs straight and prorsiradiate, fasciculate, branching in mid- to just above the mid-flank into usually three secondary ribs. Intercalatory secondary ribs also present.

MEASUREMENTS

Maximum diameter 65mm; septate diameter 37mm; maximum whorl height 26mm, width 21mm; no of ribs c.27 primary, about 75 secondary.



FIG. 3. *Galbanites* (*Galbanites*) *galbanus* Buckman, 1922, internal mould showing detail of suture, QM F1270. At left are moulds of '*Leptomaria*' *rugata* (Benett, 1831) artificially cemented to the umbilicus. $\times 1$.

REMARKS

The specimen of *G. fasciger* differs from *G. galbanus* by being smaller, more involute, flatter sided and having fasciculate ribs. The ribbing is more regularly prorsiradiate. Wimbledon (1974: 72) believed that *G. fasciger* represented the inner/juvenile whorls of *Briarites polymeles* Buckman or a closely related species.

Class GASTROPODA

Family PLEUROTOMARIIDAE Swainson, 1844

Leptomaria Eudes-Deslongchamps, 1864

Type species. Pleurotomaria amoena Eudes-Deslongchamps, 1849, Bajocian, Middle Jurassic, France.

'*Leptomaria*' *rugata* (Benett, 1831)
(Figs 1, 3) (Fig. 1, centre; Fig. 3, left)

1831 *Trochus rugatus* Benett, p.6, pl.16, upper right.

1888 *Pleurotomaria rugata* Benett; Damon, pl.8, fig.

11.

1909 *Leptomaria* (?) sp.; Etheridge, p.239, pl.68.

1927 *Leptomaria* (?) sp.; Whitehouse, p.111.

1946 *Leptomaria* (?) sp.; Whitehouse, p.3.

1989 *Trochus rugatus* Benett; Spamer, Bogan & Torrens, p. 141 [q.v. for further synonymy].

MATERIAL EXAMINED

SYNTYPE: Original of Benett (1831: pl.16) upper right figure, Academy of Natural Science, Philadelphia, 65710 (B.C. 506), fide Spamer et al. (1989), Portland Beds, Tisbury, Wiltshire.

OTHER MATERIAL: Four specimens: QM F21078-21081, artificially cemented to the umbilicus of QM F1270.

REMARKS

The smooth internal moulds have the apices broken off, but would have had a blunt apical angle; there are traces of a weak shoulder. The preservation is typical of '*L. rugata*' in the Portland Beds of England.

CONCLUSIONS

The two ammonites, reported to be from the Early Cretaceous of Victoria Downs, Queensland, formerly attributed to Hauterivian *Simbirskites* (Whitehouse, 1926, 1927, 1946), are confirmed, along with associated bivalves and gastropods, as English, Late Jurassic, Portland

Stone forms. *Galbanites* (*Galbanites*) *galbanus* and *G. (G.) fasciger* suggest Portlandian/Tithonian faunas 3/4, the *okusensis/kerberus* zones of Wimbledon & Cope (1978) and Cope et al. (1980). The Cockly Bed of the former Okus Quarry in Swindon, Wiltshire, is probably the most likely original site, but is not proven. The gastropod '*Leptomaria*' *rugata* and the bivalves, including *Laevitrigonia damoniana* and oysters associated with the ammonites are also common in the Cockly Bed. The record of *Simbirskites* from Australia should now be deleted. The provenance of other material of the Hurst/Hunter bequest should be treated with caution.

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NEW INFORMATION ON THE AUSTRALIAN SMALL BITTACIDS (MECOPTERA)

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The unrecorded male and additional females of the small and little known scorpion-fly *Symbittacus scitulus* Byers have been found at three north Queensland montane rainforest localities. The male terminalia are similar to those of *Edriobittacus* Byers. New localities for the other small Australian bittacids show that *Austrobittacus anomalus* Riek occurs in the coastal zone between Bundaberg and Rockhampton, *Tythobittacus macalpinei* Smithers extends into south-east Queensland, and *Edriobittacus microcercus* (Gerstaecker) is widely distributed between Bundaberg and Cairns. □ *Mecoptera*, *Bittacidae*, *Edriobittacus*, *Tythobittacus*, *Austrobittacus*, *scorpion-fly*, *rainforest*, *Queensland*, *new records*.

Kevin J. Lambkin, Queensland Museum, P.O. Box 3700, South Brisbane, Queensland 4101, Australia; 6 November, 1992.

The Australian bittacid fauna comprises 6 genera. The monotypic *Austrobittacus* Riek, *Edriobittacus* Byers, *Symbittacus* Byers and *Tythobittacus* Smithers are small and delicate forms, which have AA_{3+4} (=1A of other notations) of the hindwing much reduced. *Bittacus* Latreille (1 species) and *Harpobittacus* Gerstaecker (9 nominal species) are large and robust scorpion-flies with AA_{3+4} of the hind wing well developed. Byers (1986) provided a key to all genera except *Bittacus*, which was differentiated by Lambkin (1988).

Symbittacus was erected by Byers (1986) for *S. scitulus* Byers, which was based on one female from rainforest of Bellenden-Ker Range, north Queensland. Since then, further collecting by G.B. Monteith and colleagues in montane rainforest south of Bellenden-Ker has brought to light a further five specimens, including the first male. An examination of the collections of the Australian National Insect Collection, Canberra (ANIC) has also revealed a female specimen from another north Queensland rainforest locality. Herein I record this new material and describe the male. As well, new diagnostic characters and new localities are given for *Austrobittacus*, *Edriobittacus* and *Tythobittacus*. No new localities have been published for these taxa since their original descriptions or since Riek (1954). Full reference lists for each have recently been given by Smithers (1987) and are not repeated here.

All measurements are in millimetres. Other abbreviations used are as follows: ICZN, International Code of Zoological Nomenclature; KJL, author's collection (to be deposited in Queensland Museum); LFW, fore wing length; MV, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; UQ, The University of

Queensland Insect Collection, Department of Entomology, University of Queensland.

Symbittacus scitulus Byers (Figs 1A-C,2)

Symbittacus scitulus Byers, 1986, pp. 166-168, figs 1-6.

MATERIAL EXAMINED

QUEENSLAND: QM: 1♂, 1♀ (both teneral), Cardwell Range, Upper Broadwater Ck valley, 700-800m, RF [rainforest], 17-21.iii.1986, 3♀♀, Kirrama Range, Douglas Ck road, 800m, 9-12.xii.1986, all G.Monteith, G.Thompson and S.Hamlet. ANIC: 1♀, Davies Ck, 20km E by S Mareeba, 20.xi.1981, D.H.Colless, Malaise trap

LFW

♂ 14.9, ♀♀ 14.1-14.6 (holotype recorded by Byers (1986) as 14.1).

MALE TERMINALIA (Fig. 1A-C)

Epiandrium short, plate-like, articulated on the anterodorsal corners of sternum 9; in lateral view (Fig. 1A) narrow, arched dorsally at c.2/3 length; in dorsal view (Fig. 1B) posterior margin broadly incised to c.2/3 length, resultant lobate paired lateral regions each with 5 short black spines medioapically. Posterior margin of sternum 9 with a few long setae dorsally. Basistyles completely fused medially; in lateral view ventro-posterior margin evenly curved; dististyle-bearing lobes strongly produced. Dististyle (Fig. 1C) small and simple, with strongly sclerotised glabrous apical knob; distinct 'stylocavemula' (Tjeder 1970) basally. Aedeagus of moderate length, recurved, without a terminal



FIG. 1. A-C (0.5mm scale line). *Symbittacus scitulus*, male: A, apex of abdomen, left lateral; B, epiandrium, dorsal; C, right dististyle, posteroventral (darker circular area is the 'stylocavernula'). D,E (2mm scale line). Distal regions of right fore and hind wings (venation only shown): D, *Edriobittacus microcercus*; E, *Tythobittacus macalpinei*. Abbreviations: Aed, aedeagus; Bs, basistyles; C, cercus; Epi, epiandrium; S8,9,11, sterna 8,9,11; T8,11, terga 8,11.

filamentous extension. Tergum 10 not detected (specimen teneral). Cercus elongate, reaching to level of dististyle; broadest at c. $\frac{1}{2}$ length, then tapering distally. Tergum 11 elongate, in posterior perpendicular view tapering to an acute apex. Sternum 11 much shorter than tergum 11, with apical margin truncate.

REMARKS

The new material compares well with Byers' (1986) description, but 2 minor variances can be noted. Byers recorded the ocelli as of uniform diameter. In all the new material (and, on re-examination, in the holotype as well) the lateral ocelli are slightly larger than the medial one. The number of thick black setae on each side of the 4th hind tarsomere, recorded as 1 by Byers, is variable. The holotype and one of the Kirrama females (both with fore wings 14.1 long) have 1 or 2, whereas the other specimens (which are larger) have 2. Unfortunately the male is teneral and not well preserved, but its non-genital structural features are similar to those of the female.

The male terminalia of *S. scitulus* are similar to those of *Edriobittacus microcercus* (Gerstaecker) (Byers, 1974, figs 1-3). The latter differ, however, in the following: 1, the epiandrium in lateral view is arched before midlength (at c. $\frac{2}{3}$ length in *Symbittacus*), and more strongly so than in *Symbittacus*; in dorsal view it is much more deeply incised than in *Symbittacus*; 2, the aedeagus is longer; 3, there are numerous (rather than a few as in *Symbittacus*) long setae on the posterior margin of sternum 9; 4, tergum 11 is short with the apical margin truncate (elongate with apex acute in *Symbittacus*).

Symbittacus scitulus is a rainforest scorpionfly. It has only been taken at elevations of 700-800m. The specimens from Cardwell and Kirrama Ranges were collected at night while at rest on the foliage of understorey vegetation along tracks through rainforest (G.B. Monteith, pers. comm.).

Austrobittacus anomalus Riek (Fig. 2)

Austrobittacus anomalus Riek, 1954, p.157, figs 3,4, pl.1, fig.6.

MATERIAL EXAMINED

QUEENSLAND: ANIC: holotype ♂, allotype ♀, 1 without abdomen, 4 ♂ and 10 ♀ paratypes, Rockhampton, 23.iii.1950, 1 ♀ paratype, Olsen's Caves, 13 miles

N Rockhampton, 25.iii.1950, all I.F.B. Common; 1 ♂, 3 ♀ ♀, Pine Ck, 12 miles S Bundaberg, 12.iii.1976, 14.iv.1976, 1 ♂, Monduran Dam, 20km N Gin Gin, 2.ii.1974, all H.Frauca. KJL: 5 ♂ ♂, 6 ♀ ♀, Bruce Highway, Rosedale turnoff, 10km NW Gin Gin, 4 ♂ ♂, 6 ♀ ♀, near 'Wakelin', 20km NNW Gin Gin, all 20.iv.1985, K.J. and C.L.Lambkin.

LFW

♂ ♂ 14.0-15.3, ♀ ♀ 13.8-14.6 (Riek (1954) recorded 15.0 for the species).

REMARKS

Riek (1954) did not explicitly state which specimens were the holotype, allotype or paratypes. The holotype and allotype are labelled as such, but none of Riek's other specimens are labelled as paratypes. Riek did not, however, expressly exclude any of his specimens from the



FIG. 2. Distribution of *Symbittacus scitulus* and *Austrobittacus anomalus*.

type series (see ICZN Article 72(b)(i)), and I believe that there is sufficient evidence (see ICZN Recommendation 72B) to regard the 16 specimens listed above as paratypes (viz the collection data match those given by Riek, and the Olsen's Caves specimen matches that illustrated by Riek (1954, pl.1, fig.6) and stated to be a paratype in the figure caption).

This species is easily distinguished by the longitudinal form of the free apical portion of AA_{3+4} in the hind wing (Byers, 1991, fig.37.6C). The lateral ocelli are slightly larger than the medial one. The number of thick black setae on each side of the 4th hind tarsomere, recorded by Byers (1974) as 4-5, ranges from 2 to 7 and can vary from side to side in the same specimen.

All specimens have been taken in late summer or autumn. The Rosedale turnoff and Wakelin specimens were collected in the grass under-

storey of eucalypt woodland in company with *Edriobittacus microcercus* (at Wakelin only) and *Harpobittacus scheibeli* Esben-Petersen.

***Edriobittacus microcercus* (Gerstaecker)**
(Figs 1D,3)

Bittacus microcercus Gerstaecker, 1885, p.119.

Kalobittacus microcercus: Riek, 1954, pp.155-156, figs 1,2.

Edriobittacus microcercus: Byers, 1974, pp.165-167, figs 1-4.

MATERIAL EXAMINED

QUEENSLAND: ANIC: 1♂, 12 miles E Duaringa, 18.iii.1958, 4♂♂, 1♀, 25 miles N Gin Gin, 16(1♂) and 23.iii.1958, 2♂♂, 1♀, Hedlow Ck, nr Yeppoon, 22.iii.1958, all I.F.B.Common; 1♀, Ingham, 29.iii.1961, K.L.S.Harley; 1♂, Mackay, 17.v.1969, [G.F.] Bornemissza, 'flew to light'; 1♀, 63 miles N Marlborough, 9.v.1955, K.R.Norris; 1♂, Olsen's Caves, 13 miles N Rockhampton, 25.iii.1950, I.F.B.Common; 1♂, Palm Grove [?Cove], nr Cairns, June 1969, R.Hardie; 1 without abdomen, Pine Ck, 12 miles S Bundaberg, 12.iii.1976, 1♀, Pinock R, Hogback Range, WSW Bundaberg, via Gin Gin, 11.iii.1972, all H.Frauca; 1♀, 7 miles NNE Ravenshoe, 3300', 22.iv.1969, I.F.B.Common and M.Upton; 1 without abdomen, Rockhampton; 1♂, The Caves, 16 miles N Rockhampton, 3.iv.1967, M.S.Upton. KJL: 1♂, near 'Wakelin', 20 km NNW Gin Gin, 20.iv.1985, K.J. and C.L.Lambkin. UQ: 1♀, Walkamin, Atherton Tableland, August 1967, P.H.Twine. MV: 3♂♂, 3♀♀, 1 without abdomen, 'Queensland'.

LFW

♂♂ 16.3-19.7 (holotype recorded by Esben-Petersen (1921) as 18.0), ♀♀ 17.1-19.5

REMARKS

Both sexes have the lateral ocelli much larger than the medial one (noted in the male only by Byers, 1974), and the number of thick black setae on each side of the 4th hind tarsomere, recorded by Byers (1974) as 3, ranges from 2 to 5.

The holotype was from Peak Downs. The only other previous records are those of Riek (1954): the Olsen's Caves specimen in the ANIC, and the series labelled 'Queensland' in the MV. All specimens have been taken from March to August.



FIG. 3. Distribution of *Edriobittacus microcercus* and *Tythobittacus macalpinei*.

***Tytthobittacus macalpinei* Smithers**
(Figs 1E,3)

Tytthobittacus macalpinei Smithers, 1973, p.300, figs 9-11.

MATERIAL EXAMINED

NEW SOUTH WALES: KJL: 1♂, Terania Ck, 22.i.1986, L.Müller and G.Theischinger. QUEENSLAND: UQ (all in poor condition): 1♂, 1♀, Brisbane, 8.x.1959, F.Lamberth, 9.x.1966, E.Rainey; 1♀, Kenilworth State Forest, 5.xii.1966, G.B.Monteith, 'sweeping ferns in rainforest'; 1♂, Mt Coot-tha, Brisbane, 26.ix.1959, A.J.Jackson.

LFW

Terania Ck ♂ 13.3 (Smithers, 1973, recorded 14.0 for the species).

REMARKS

T. macalpinei is very similar in wing venation to *E. microcercus*. Further to Byers (1986), it can be distinguished by its smaller size (LFW c.13.0-14.0, vs at least 16.3 in *E. microcercus*) and two series of crossveins in the distal region of both wings (Fig. 1E) compared to three in *E. microcercus* (Fig. 1D). The latter character is particularly useful in identifying faded or teneral females, which Byers' key will not separate. The lateral ocelli are slightly larger than the medial one and there are 1-3 thick black setae on each side of the 4th hind tarsomere.

Smithers' (1973) material was all from New South Wales: Huonbrook, Mooney Mooney Creek, Mt Wilson and Wentworth Falls. The Terania Creek and Kenilworth specimens were both taken in rainforest, the former in flight along a creek bed (G. Theischinger, pers. comm.) and the latter swept from ferns. The records from Brisbane and Mt Coot-tha, not obvious rainforest localities, are based on student collections and could be doubtful. All specimens have been taken from September to March.

ACKNOWLEDGEMENTS

I appreciate the cooperation of Josephine Cardale (ANIC), Ken Walker (MV) and Margaret Schneider (UQ) in making available specimens under their care. Christine Lambkin drew Fig. 1A-C for which I am very grateful.

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FREQUENCY OF OBSERVATION OF BIRD SPECIES IN SUB-COASTAL FARMLAND IN SOUTHEAST QUEENSLAND

G.J. LEACH AND H.B. HINES

Leach, G.J. & Hines, H.B. 1993 06 30: Frequency of observation of bird species in sub-coastal farmland in southeast Queensland. *Memoirs of the Queensland Museum* 33(1): 259-275. Brisbane. ISSN 0079-8835.

A farming district in southeast Queensland was surveyed from June 1980 to May 1985 to determine presence of bird species. Softwood scrub was the predominant vegetation before European settlement, but now occurs only in isolated remnant patches. Standard surveys were conducted on 20 days, one per season per year, and other surveys on another 100 days. The district supports a diverse and abundant avifauna: 44 waterbird, 60 non-passerine landbird and 88 passerine species.

Nearly 40% of waterbird and passerine species observed in standard surveys were observed in over 80% of them, but only 21% of non-passerine landbird species. In contrast, 45% of the latter species were observed on 20% or fewer visits, compared with 25% of the waterbird and passerine species. Frequency of several waterbird species was minimum in the wettest year, following widespread drought in southeast Australia.

Thirty species had large differences in mean seasonal frequency; some were summer or winter visitors. Approximate dates of presence are given. Rose Robin, Grey Fantail and Yellow-faced Honeyeater were present during well-defined winter periods, while Rufous Fantail and several other species were summer visitors. Scarlet Honeyeater and Spotted Pardalote were passage migrants.

The combination of standard and other surveys generated a robust database against which changes in relative abundance can, and should, be monitored to guide management. While an effective habitat mosaic remains for passerines and waterbirds, it appears less suitable for non-passerine landbirds other than doves and parrots which can be commensal with farming. Retention and better management of native woody vegetation may be essential to forestall decline in the avifauna with more intensive settlement. □ *Bird, farmland, habitat, remnant vegetation, seasonal movement, management.*

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Since European settlement, the vegetation of Australia has been progressively cleared and modified. This has led to decreases and actual losses of fauna and flora (Saunders, 1989; Hobbs & Hopkins, 1990; Recher & Lim, 1990; Saunders & Curry, 1990). Despite these changes, agricultural landscapes may be significant wildlife habitats (Breckwoldt, 1983, 1986; Saunders et al., 1987). Remnant vegetation along roadsides, for example, is used by many species of birds (Arnold & Weeldenburg, 1990; Cale, 1990; Saunders & de Rebeira, 1991; Leach & Recher, 1993).

Various workers have reported census data from avian communities in relatively undisturbed forest, woodland and heathland (e.g. Kikkawa, 1982; Pyke, 1983, 1988; Recher et al., 1985; Ford et al., 1985; Gosper, 1992; see also Keast et al., 1985; Ford, 1989). By contrast, information from highly modified landscapes is often anecdotal (e.g. Barnard, 1925; Lord, 1956) and comparisons of historical and present day abundances based on 'reporting rates' (Blakers et al., 1984)

are insufficient for the needs of management because the data are compiled at too coarse a scale (Ford, 1989).

In this paper, we report five years of census data from the Marburg district, a subcoastal farming area of southeast Queensland. The district includes a diverse mosaic of habitats and is rich in bird species (Leach & Hines, 1987). The data concern (1) the relative abundances of bird species and (2) seasonal changes in their abundances. They provide a baseline that will permit assessment of future changes in the avifauna as land management practices alter or intensify.

English names for birds follow those of R.A.O.U. (1978).

STUDY AREA AND METHODS

THE SURVEY AREA

The survey area was the 10' grid square centred on 27°35'S, 152°35'E (Fig 1a). Marburg is near the centre and Rosewood, with a population of

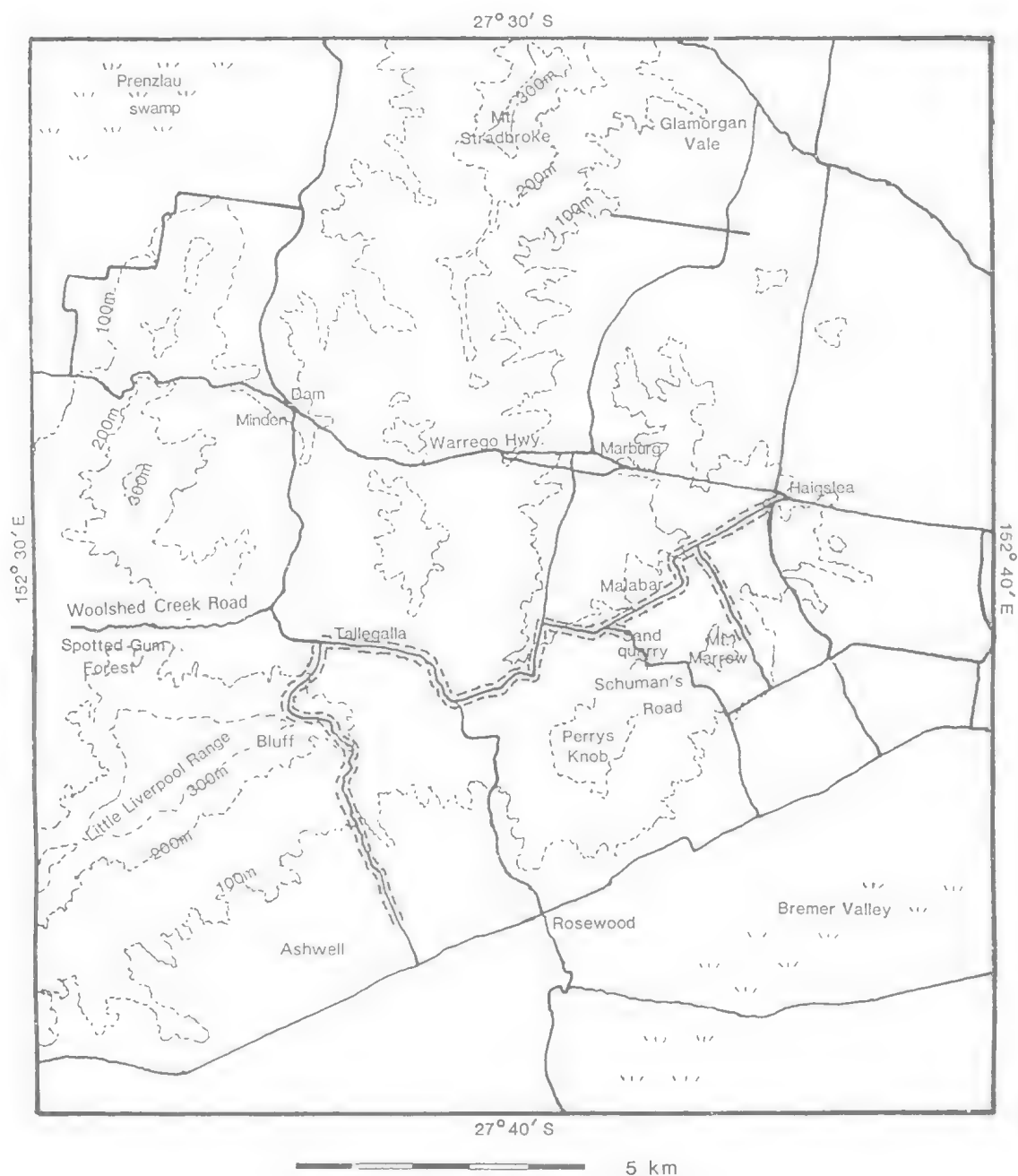
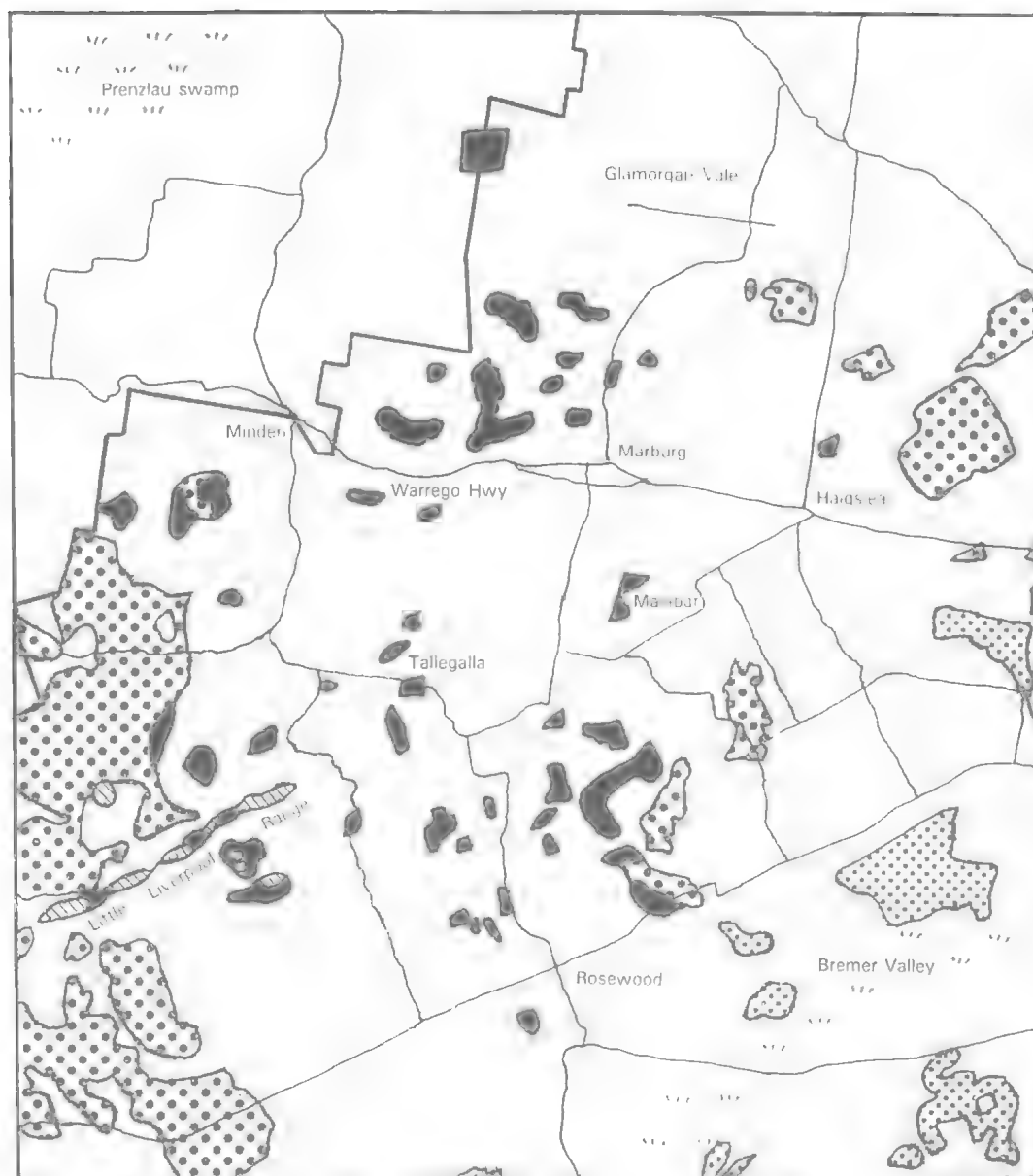


FIG. 1. The Marburg district showing (this page) the standard survey route (---), physiography and other features mentioned in the text and (next page) remnants of forest and woodland vegetation in the area of the grid square within Moreton Shire (after Young, 1985, courtesy of P.A. Young and Moreton Shire Council). An equivalent map is not available for the area beyond the shire boundary (the heavy line in the north-west) but distribution of vegetation remnants through the landscape, excluding the ephemeral swamp at Prenzlau, is not markedly dissimilar. Note that the widespread narrow galleries of vegetation along roadsides and fencelines are not shown.







-  Brigalow-software closed-forest.
-  Softwood-Hoop Pine (*Araucaria cunninghamii*) closed forest.
-  Eucalypt open-forest (Spotted gum, ironbarks; Gum-topped Box, *E. moluccana*, northeast of Haigslea).
-  Eucalypt woodland (Blue Gum, *E. tereticornis*, and ironbarks).

TABLE 1. Mean seasonal frequency (MSF) in standard surveys, and mean annual frequency (MAF) in standard surveys and other surveys, for waterbird species. Species are tabulated in descending order of MAF first in the standard surveys and subsidiarily in other surveys. Seasons are: Wi, winter; Sp, spring; Su, summer; Au, autumn. Range, the difference between maximum and minimum annual frequency. Years, the number of years, in parentheses, in which species were observed.

Species	Standard surveys							Other surveys		
	Wi	Sp	Su	Au	MAF	Range	Years	MAF	Range	Years
Australasian Grebe	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.98	0.11	(5)
Pacific Black Duck	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.96	0.11	(5)
Dusky Moorhen	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.95	0.12	(5)
Cattle Egret	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.91	0.15	(5)
Little Pied Cormorant	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.86	0.07	(5)
Eurasian Coot	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.83	0.35	(5)
White-faced Heron	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.80	0.37	(5)
Masked Lapwing	1.00	0.80	1.00	1.00	0.95	0.25	(5)	0.92	0.15	(5)
Little Black Cormorant	0.80	1.00	1.00	1.00	0.95	0.25	(5)	0.82	0.26	(5)
Purple Swamphen	1.00	1.00	0.80	1.00	0.95	0.25	(5)	0.79	0.32	(5)
Grey Teal	1.00	0.80	1.00	0.80	0.90	0.28	(5)	0.58	0.36	(5)
Hardhead	1.00	1.00	1.00	0.60	0.90	0.25	(5)	0.53	0.26	(5)
Straw-necked Ibis	0.80	0.60	0.80	1.00	0.80	0.50	(5)	0.74	0.55	(5)
Black-winged Stilt	0.60	0.60	0.80	0.60	0.65	0.25	(5)	0.47	0.53	(5)
Royal Spoonbill	0.60	0.60	0.80	0.60	0.65	1.00	(4)	0.35	0.46	(5)
Black-fronted Plover	0.60	0.80	0.60	0.60	0.65	0.75	(5)	0.28	0.48	(5)
Intermediate Egret	0.80	0.60	0.60	0.40	0.60	1.00	(4)	0.56	0.32	(5)
Pacific Heron	0.80	0.20	0.60	0.40	0.50	0.80	(5)	0.42	0.42	(5)
Comb-crested Jacana	0.60	0.40	0.40	0.60	0.50	0.75	(4)	0.33	0.67	(5)
Sacred Ibis	0.20	0.20	0.60	0.80	0.45	0.75	(4)	0.46	0.47	(5)
Maned Duck	0.60	0.40	0.40	0.40	0.45	0.50	(5)	0.40	0.17	(5)
Plumed Whistling-Duck	-	0.60	0.20	0.60	0.40	0.75	(3)	0.34	0.46	(5)
Latham's Snipe	-	0.80	0.80	-	0.40	0.50	(4)	0.24	0.26	(5)
Great Egret	0.40	0.60	-	0.20	0.30	0.75	(3)	0.39	0.42	(5)
Yellow-billed Spoonbill	0.40	-	0.20	0.20	0.20	0.25	(4)	0.27	0.51	(5)
Darter	0.20	-	0.20	0.40	0.20	0.50	(3)	0.14	0.14	(5)
Red-kneed Dotterel	0.20	0.20	0.20	0.20	0.20	0.75	(2)	0.10	0.28	(3)
Pink-eared Duck	0.20	0.40	-	0.20	0.20	0.50	(3)	0.07	0.16	(4)
Glossy Ibis	-	0.20	0.20	-	0.10	0.25	(2)	0.19	0.56	(3)
Little Egret	0.20	-	0.20	-	0.10	0.25	(2)	0.05	0.17	(3)
Australian Pelican	0.20	-	-	-	0.05	0.25	(1)	0.13	0.19	(4)
Great Cormorant	-	-	-	0.20	0.05	0.25	(5)	0.02	0.06	(5)
Black Swan	-	-	-	-	-	-	-	0.19	0.61	(4)
Australasian Shoveler	-	-	-	-	-	-	-	0.10	0.33	(4)
Little Bittern	-	-	-	-	-	-	-	0.06	0.07	(5)
Rufous Night Heron	-	-	-	-	-	-	-	0.03	0.06	(3)
Sharp-tailed Sandpiper	-	-	-	-	-	-	-	0.03	0.16	(1)
Whiskered Tern	-	-	-	-	-	-	-	0.03	0.11	(2)
Black-necked Stork	-	-	-	-	-	-	-	0.02	0.06	(2)
Wandering Whistling-Duck	-	-	-	-	-	-	-	0.02	0.05	(2)
Chestnut Teal	-	-	-	-	-	-	-	0.02	0.11	(1)
Buff-banded Rail	-	-	-	-	-	-	-	0.02	0.05	(2)
Pied Cormorant	-	-	-	-	-	-	-	0.01	0.06	(1)
Painted Snipe	-	-	-	-	-	-	-	0.01	0.06	(1)

1657, is the main town. Physiography, vegetation and land use are described by Leach & Hines (1987). The landscape, of low hills (max elevation: 396m) and broad valleys, has been substantially cleared for agriculture, other rural use and residential occupation. There are creeks that flow intermittently, small swamps and numerous farm dams.

Fertile prairie soils and grey cracking clays are common. In the past they supported low closed-forest and brigalow (*Acacia harpophylla*)-softwood closed-forest which covered about half the

survey area (Anonymous, 1974; Young, 1985; Hass, 1987; Young & McDonald, 1987; Elsoll, 1991). We describe these two vegetation types as softwood scrub; remnants are now patchily distributed and occupy less than 4% of the area (Fig. 1b). Many of the remnants are substantially disturbed. Thin solodic soils on some low hilly terrain support open eucalypt forest (Spotted Gum, *Eucalyptus maculata*, and the ironbarks *E. crebra* and *E. melanophloia* are common); these associations now cover about 9% of the district.

WEATHER

Weather records for Lawes, 15 km west of the survey area, show a mean annual rainfall of 780 ± 183 mm (83 years) with 70% falling in October through March (Cook & Russell, 1983; Willcocks & Young, 1991). Mean monthly maximum temperatures range from 20.3°C in July to 31.0°C in December, and mean monthly minimum temperatures from 5.6°C in July to 19.1°C in February. On average, light frosts (screen minimum 0.1 to 2.2°C) occur on 12.5 days and heavy frosts (screen minimum 0.0°C or lower) on 2.3 days per year.

Between 1980 and 1985 annual rainfall (June through May) ranged from 697 mm to 951 mm. Seasonal variability was high with 23 mm in June through August 1982 and 419 mm in December through February 1981–82. In most seasons rainfall was near or below average but in March through May 1983, and June through August 1983 and 1984, rainfall exceeded the average by over 50% (Leach & Hines, 1992). Mean maximum monthly temperatures were $>1^\circ\text{C}$ above average from August through November 1980, in February and March 1983, in December 1984 and in January 1985 and were $>1^\circ\text{C}$ below average from September through November 1984. Minimum temperatures were $>1^\circ\text{C}$ above average from November 1981 through January 1982 and from May through October 1983 and were $>1^\circ\text{C}$ below average in June and July 1982. From June through August there were 17 light, and five severe, frosts in 1982, 11 light frosts in 1981, six in 1980 but only two in both 1983 and 1984.

SURVEY PROCEDURES

From June 1980 through May 1985 we surveyed birds along a standard route once each season (20 standard surveys). (Seasons are as follows: winter, June through August; spring, September through November; summer, December through February; autumn, March through May). The 20 km route, from Haigslea to Ashwell (Fig. 1a), was traversed between 0730 and 1200 h. At eight sites foot surveys of 10 to 45 minutes were conducted (Appendix 1); additional observations were made during the 5 to 15 minute periods driving between sites. Mid-afternoon surveys of Minden Dam and its surroundings (Fig. 1a) were included in the standard survey. Surveys were conducted by two to four observers who listed all species of bird seen or heard. The main habitats sampled were open farmland (predominantly pasture with isolated acacia and other trees), degraded softwood scrub remnants,

woody weeds along roadsides and fencelines, and farm dams.

In addition to the 20 standard surveys, the Marburg district was visited on another 100 days, usually between about 0700 h and 1600 h. Surveys conducted on these days are referred to as 'other surveys' though some wholly or partly overlapped the route of standard surveys. There were 18 visits in both winter and summer periods, 32 in both spring and autumn periods, and between 17 and 26 each year. Most observations were made while walking or driving slowly along secondary roads and bush tracks. G.J.L. was on all surveys and was usually accompanied by one or more experienced observers. Appendix 2 lists the principal areas visited, the frequency of visits and the main habitats represented. These surveys differed from the standard surveys in that eucalypt associations were often traversed.

DATA COLLATION

The likelihood that a species was present in the survey area was estimated for each species as: (number of visits on which the species was observed)/(total number of visits). Values were calculated for each season of each year (seasonal frequency) and for each year (annual frequency). Mean Seasonal Frequency (MSF) and Mean Annual Frequency (MAF) were derived from the five years of observations. Data from the standard surveys and from the other surveys are treated separately. Species with $\text{MAF} > 0.2$ in the standard surveys are referred to as *principal* species. The difference between maximum and minimum annual frequency is used as a measure of variation across years. It is more useful than standard error, especially when means are based on observations from only one or two years.

In this report, waterbirds include all species of Podicipedidae, Pelecanidae, Anhimidae, Phalacrocoracidae, Ardeidae, Ciconiidae, Plataleidae, Anatidae, Rallidae, Jacanidae, Rostratulidae, Charadriidae, Recurvirostridae, Scolopacidae and Laridae. Other non-passerines are referred to as non-passerine landbirds.

RESULTS

SPECIES OBSERVED

One hundred and thirty one species were observed in the standard surveys and 190 in other surveys (Tables 1–3). All species observed in the standard surveys, except Rose-crowned Fruit-Dove and Forest Kingfisher, were also observed in the other surveys. Thus, the total number of

TABLE 2. Mean seasonal frequency (MSF) in standard surveys, and mean annual frequency (MAF) in standard surveys and other surveys, for non-passerine landbird species. Species order and abbreviations are as in Table 1.

Species	Standard surveys							Other surveys		
	Wi	Sp	Su	Au	MAF	Range	Years	MAF	Range	Years
Crested Pigeon	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.99	0.06	(5)
Australian Kestrel	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.85	0.17	(5)
Bar-shouldered Dove	1.00	0.80	1.00	1.00	0.95	0.25	(5)	0.98	0.06	(5)
Peaceful Dove	1.00	1.00	1.00	0.80	0.95	0.25	(5)	0.96	0.11	(5)
Pale-headed Rosella	1.00	1.00	0.80	1.00	0.95	0.25	(5)	0.93	0.29	(5)
Feral Pigeon	1.00	1.00	1.00	0.80	0.95	0.25	(5)	0.82	0.42	(5)
Spotted Turtle-Dove	0.80	0.80	1.00	0.80	0.85	0.25	(5)	0.81	0.35	(5)
Pheasant Coucal	0.80	0.80	1.00	0.80	0.85	0.50	(5)	0.66	0.34	(5)
Rainbow Bee-eater	0.80	0.80	0.60	1.00	0.80	0.75	(5)	0.81	0.41	(5)
Laughing Kookaburra	1.00	0.60	0.40	0.80	0.70	0.50	(5)	0.94	0.12	(5)
Scaly-breasted Lorikeet	0.80	0.60	0.40	0.40	0.55	0.50	(5)	0.67	0.36	(5)
Galah	0.40	0.80	0.60	0.20	0.50	0.50	(5)	0.49	0.24	(5)
Common Koel	-	0.80	1.00	-	0.45	0.25	(5)	0.30	0.24	(5)
Black-shouldered Kite	0.80	0.60	0.20	0.20	0.45	0.50	(5)	0.25	0.11	(5)
Sacred Kingfisher	0.20	0.80	0.60	-	0.40	0.25	(5)	0.51	0.18	(5)
Cockatiel	0.60	0.40	0.20	0.40	0.40	0.50	(5)	0.39	0.15	(5)
Wedge-tailed Eagle	0.80	0.20	-	0.60	0.40	0.50	(5)	0.26	0.23	(5)
Brown Falcon	0.40	0.20	0.20	0.40	0.30	0.25	(5)	0.27	0.34	(5)
Dollarbird	-	0.40	0.60	-	0.25	0.50	(4)	0.40	0.07	(5)
Brown Quail	-	0.40	0.40	0.20	0.25	0.75	(2)	0.15	0.44	(4)
Horsfield's Bronze-Cuckoo	-	0.60	0.40	-	0.25	0.50	(4)	0.11	0.17	(4)
Channel-billed Cuckoo	-	0.60	0.20	-	0.20	0.50	(3)	0.25	0.20	(5)
Brush Cuckoo	-	0.20	0.60	-	0.20	0.50	(3)	0.23	0.14	(5)
Brown Goshawk	0.40	0.20	-	0.20	0.20	0.50	(4)	0.09	0.12	(4)
Common Bronzewing	-	0.20	-	0.20	0.10	0.50	(1)	0.13	0.24	(4)
Azure Kingfisher	-	-	-	0.40	0.10	0.25	(2)	0.07	0.15	(3)
Pallid Cuckoo	-	0.40	-	-	0.10	0.25	(2)	0.04	0.18	(2)
Spotted Harrier	0.40	-	-	-	0.10	0.25	(2)	0.02	0.06	(2)
White-throated Needletail	-	-	0.40	-	0.10	0.25	(2)	0.02	0.06	(2)
Fan-tailed Cuckoo	-	0.20	-	-	0.05	0.25	(1)	0.26	0.19	(5)
Shining Bronze-Cuckoo	-	0.20	-	-	0.05	0.25	(1)	0.19	0.45	(4)
Stubble Quail	-	-	0.20	-	0.05	0.25	(1)	0.13	0.26	(3)
Rainbow Lorikeet	0.20	-	-	-	0.05	0.25	(1)	0.09	0.18	(4)
Australian Hobby	-	0.20	-	-	0.05	0.25	(1)	0.05	0.18	(3)
Peregrine Falcon	-	0.20	-	-	0.05	0.25	(1)	0.02	0.11	(1)
Grey Goshawk	-	-	0.20	-	0.05	0.25	(1)	0.01	0.05	(1)
Rose-crowned Fruit-Dove	-	-	0.20	-	0.05	0.25	(1)	-	-	-
Forest Kingfisher	-	-	-	0.20	0.05	0.25	(1)	-	-	-
Little Lorikeet	-	-	-	-	-	-	-	0.26	0.19	(5)
Whistling Kite	-	-	-	-	-	-	-	0.10	0.39	(4)
Blue-winged Kookaburra	-	-	-	-	-	-	-	0.07	0.22	(3)
Pacific Baza	-	-	-	-	-	-	-	0.06	0.11	(4)
Painted Button-quail	-	-	-	-	-	-	-	0.05	0.17	(2)
Emerald Dove	-	-	-	-	-	-	-	0.05	0.11	(3)
Collared Sparrowhawk	-	-	-	-	-	-	-	0.04	0.10	(3)
White-bellied Sea-Eagle	-	-	-	-	-	-	-	0.04	0.22	(1)
Marsh Harrier	-	-	-	-	-	-	-	0.04	0.17	(2)
Tawny Frogmouth	-	-	-	-	-	-	-	0.04	0.18	(2)
Australian Brush-turkey	-	-	-	-	-	-	-	0.03	0.06	(3)
Australian King-Parrot	-	-	-	-	-	-	-	0.03	0.11	(2)
Little Bronze-Cuckoo	-	-	-	-	-	-	-	0.03	0.06	(3)
Sulphur-crested Cockatoo	-	-	-	-	-	-	-	0.02	0.06	(2)
Musk Lorikeet	-	-	-	-	-	-	-	0.02	0.12	(1)
Crimson Rosella	-	-	-	-	-	-	-	0.02	0.08	(1)
Little Eagle	-	-	-	-	-	-	-	0.01	0.04	(1)
Topknot Pigeon	-	-	-	-	-	-	-	0.01	0.04	(1)
Brown Cuckoo-Dove	-	-	-	-	-	-	-	0.01	0.06	(1)
Wonga Pigeon	-	-	-	-	-	-	-	0.01	0.06	(1)
Southern Boobook	-	-	-	-	-	-	-	0.01	0.05	(1)
Barking Owl	-	-	-	-	-	-	-	0.01	0.05	(1)

species observed was 192. Tables 1, 2 & 3 separate observations for, respectively, waterbirds (44 species, 32 in standard surveys), non-passerine landbirds (60, 38) and passerines (88, 61). In each table species are ranked in descending order of MAF.

Seventy-seven species (41%, 30% and 47% of waterbirds, non-passerine landbirds and passerines, respectively) were observed every year in the standard surveys and 112 species (64%, 38% and 69%) in other surveys. Ninety-one species (55%, 35% and 52%) qualified as *principal* species.

VARIATION IN ANNUAL FREQUENCY OF OBSERVATION OF SPECIES

All species are classed according to variation in annual frequency in Table 4. In standard surveys, variation in frequency across years was low for 80 species (48 principal species). Variation was also low for 52 of these species (32 principal species) in the other surveys. In contrast, annual variation for Glossy Ibis, Yellow-billed Spoonbill, Hardhead, Black-winged Stilt, White-throated Gerygone, Zebra Finch and Pied Currawong was high in the other surveys. Seventeen species had high variation in annual frequency in standard surveys, but only Comb-crested Jacana and Common Myna were as variable in the other surveys. Most species that occurred only in the other surveys had low variation in annual frequency.

Variation in annual frequency among waterbirds, especially the shoreline species, was largely attributable to low frequencies in 1983-84.

In the standard surveys, annual frequencies of Pacific Heron decreased through the survey period ($P < 0.05$) while those of Brown Quail increased ($P < 0.05$). No consistent trends were detected across years for any other species observed in standard surveys. In other surveys, annual frequencies of eight species increased significantly through the survey period ($P < 0.05$). However, the frequencies for Plumed Whistling-Duck, Grey Shrike-thrush, Weebill, White-throated Gerygone, Buff-rumped Thornbill, White-throated Honeyeater and Pied Currawong were also related to annual variation in the frequency of visits to eucalypt forest at Tallegalla, while that for Common Myna was related to frequency of visits to both Woolshed Creek Road and Prenzlau Swamp.

Because most species (131, 68%) showed little variation in frequency between years, and much

of the variation for the remainder was correlated with the frequency of visits to specific habitats in different years, subsequent sections are concerned only with MAF and MSF values over the five years.

MEAN ANNUAL FREQUENCY (MAF)

In standard surveys, 75% of waterbird and passerine species, but only 55% of non-passerine landbird species, were principal species (Tables 1-3). More of the waterbird (38%) and passerine species (39%) than of the non-passerine landbird species (21%) were among the birds observed most regularly, i.e. in over 80% of surveys.

In the other surveys, 57, 40 and 64% of waterbird, non-passerine landbird and passerine species, respectively, were observed in over 20% of surveys; 16 to 20% of the species in these three categories were observed in over 80% of surveys.

For most species, MAF was similar in standard and other surveys. All species with high MAF (> 0.8) in standard surveys had an MAF of at least 0.5 in other surveys. Among species with intermediate MAF (0.21 to 0.80) in standard surveys, MAF in other surveys for Laughing Kookaburra, Grey Shrike-thrush, Speckled Warbler and Varied Triller was substantially greater (> 0.2 units) and that for Royal Spoonbill, Black-fronted Plover, Fairy Martin, Richard's Pipit, Red-backed Fairy-wren, Chestnut-breasted Mannikin, Tawny Grassbird and Singing Bushlark was substantially lower. Fan-tailed Cuckoo, Leaden Flycatcher, White-throated Gerygone and Pied Currawong, with low MAF (0.1 or less) in standard surveys, had MAF substantially greater in other surveys. Little Lorikeet and seven passerines that were absent from standard surveys had intermediate MAF in other surveys.

No specific family, or guild, of waterbirds was consistently observed at either high or low MAF. Among non-passerine landbirds, ground feeding pigeons and doves, including two introduced species, had high MAF, contrasting with fruit-doves which were seldom observed. Several raptors also had low MAF, but in contrast the Australian Kestrel was always observed. Among passerines, several small species (e.g. Superb Fairy-wren, Yellow Thornbill and White-browed Scrubwren) had high MAF as did the much larger, and conspicuous, Australian Magpie and Torresian Crow.

MEAN SEASONAL FREQUENCY (MSF)

Twenty-six species were observed in standard surveys in all seasons of all years and another 27

TABLE 3. Mean seasonal frequency (MSF) in standard surveys, and mean annual frequency (MAF) in standard surveys and other surveys, for passerine species. Species order and abbreviations are as in Table 1.

Species	Standard surveys							Other surveys		
	Wi	Sp	Su	Au	MAF	Range	Years	MAF	Range	Years
Willie Wagtail	1.00	1.00	1.00	1.00	1.00	0.00	(5)	1.00	0.00	(5)
Australian Magpie-lark	1.00	1.00	1.00	1.00	1.00	0.00	(5)	1.00	0.00	(5)
Australian Magpie	1.00	1.00	1.00	1.00	1.00	0.00	(5)	1.00	0.00	(5)
Torresian Crow	1.00	1.00	1.00	1.00	1.00	0.00	(5)	1.00	0.00	(5)
Superb Fairy-wren	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.99	0.06	(5)
Striped Honeyeater	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.99	0.05	(5)
Noisy Miner	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.97	0.06	(5)
Black-faced Cuckoo-shrike	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.96	0.12	(5)
Silvereye	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.96	0.10	(5)
Lewin's Honeyeater	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.95	0.12	(5)
Double-barred Finch	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.95	0.11	(5)
Pied Butcherbird	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.95	0.15	(5)
Common Starling	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.94	0.21	(5)
Figbird	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.85	0.24	(5)
Welcome Swallow	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.78	0.38	(5)
Golden-headed Cisticola	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.78	0.30	(5)
Zebra Finch	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.74	0.53	(5)
Grey Butcherbird	0.60	1.00	1.00	1.00	0.90	0.25	(5)	0.86	0.41	(5)
Yellow-rumped Thornbill	0.80	0.80	1.00	1.00	0.90	0.25	(5)	0.57	0.23	(5)
Yellow Thornbill	1.00	0.60	1.00	0.80	0.85	0.25	(5)	0.93	0.06	(5)
Rufous Whistler	0.80	1.00	0.80	0.80	0.85	0.50	(5)	0.91	0.29	(5)
White-browed Scrubwren	1.00	0.80	0.60	1.00	0.85	0.50	(5)	0.75	0.13	(5)
Clamorous Reed-Warbler	0.60	1.00	1.00	0.80	0.85	0.50	(5)	0.69	0.31	(5)
House Sparrow	0.80	0.80	1.00	0.80	0.85	0.50	(5)	0.63	0.17	(5)
Grey-crowned Babbler	0.80	0.60	0.80	1.00	0.80	0.25	(5)	0.68	0.22	(5)
Fairy Martin	0.80	1.00	1.00	0.40	0.80	0.50	(5)	0.55	0.30	(5)
Eastern Whipbird	1.00	0.80	0.60	0.60	0.75	0.50	(5)	0.70	0.48	(5)
Brown Honeyeater	1.00	1.00	0.60	0.40	0.75	0.50	(5)	0.66	0.22	(5)
Richard's Pipit	1.00	0.60	0.80	0.60	0.75	0.50	(5)	0.34	0.52	(5)
Red-backed Fairy-wren	0.80	1.00	0.60	0.60	0.75	0.75	(5)	0.34	0.29	(5)
Striated Pardalote	1.00	0.80	-	0.80	0.65	0.25	(5)	0.80	0.35	(5)
Olive-backed Oriole	0.40	0.80	0.80	0.40	0.60	0.75	(5)	0.50	0.20	(5)
Rufous Fantail	-	1.00	0.80	0.40	0.55	0.50	(5)	0.55	0.25	(5)
Grey Shrike-thrush	0.20	0.60	0.40	0.80	0.50	1.00	(5)	0.83	0.29	(5)
White-backed Swallow	0.40	0.80	0.20	0.60	0.50	0.75	(4)	0.64	0.36	(5)
Eastern Yellow Robin	0.60	0.40	0.40	0.60	0.50	0.50	(5)	0.47	0.30	(5)
Speckled Warbler	0.40	0.20	0.60	0.60	0.45	0.75	(5)	0.74	0.32	(5)
Mistletoebird	0.20	0.60	0.60	0.40	0.45	0.50	(5)	0.58	0.47	(5)
Grey Fantail	1.00	-	-	0.80	0.45	0.25	(5)	0.47	0.15	(5)
Chestnut-breasted Mannikin	0.20	0.40	0.80	0.40	0.45	0.75	(4)	0.23	0.25	(5)
Tawny Grassbird	-	0.40	1.00	0.40	0.45	0.50	(5)	0.12	0.24	(4)
Varied Triller	0.20	0.40	0.20	0.40	0.30	0.50	(3)	0.61	0.60	(5)
Common Myna	0.20	0.20	0.40	0.40	0.30	0.75	(3)	0.37	0.68	(5)
Singing Bushlark	-	-	0.80	0.40	0.30	0.25	(5)	0.08	0.24	(4)
Golden Whistler	0.80	-	-	0.20	0.25	0.00	(5)	0.37	0.20	(5)
Variegated Fairy-wren	0.40	0.60	-	-	0.25	0.50	(3)	0.32	0.41	(5)
White-winged Triller	-	0.60	0.20	-	0.20	0.25	(4)	0.08	0.15	(3)
Black-faced Monarch	-	0.20	0.20	0.20	0.15	0.50	(2)	0.13	0.26	(4)
Tree Martin	-	-	0.40	0.20	0.15	0.50	(2)	0.07	0.28	(2)
Pied Currawong	0.40	-	-	-	0.10	0.25	(2)	0.50	0.71	(5)
Spangled Drongo	0.20	-	-	0.20	0.10	0.25	(2)	0.29	0.34	(5)
Restless Flycatcher	0.20	0.20	-	-	0.10	0.25	(2)	0.12	0.41	(3)
Nutmeg Mannikin	0.20	-	-	0.20	0.10	0.50	(1)	0.11	0.24	(3)
Eastern Spinebill	0.20	-	-	0.20	0.10	0.25	(2)	0.10	0.24	(4)
White-throated Gerygone	-	0.20	-	-	0.05	0.25	(1)	0.69	0.60	(5)
Leadon Flycatcher	-	0.20	-	-	0.05	0.25	(1)	0.32	0.37	(5)
Yellow-faced Honeyeater	-	-	-	0.20	0.05	0.25	(1)	0.21	0.18	(5)
Little Friarbird	-	0.20	-	-	0.05	0.25	(1)	0.20	0.37	(5)
Red-browed Firetail	-	0.20	-	-	0.05	0.25	(1)	0.17	0.21	(5)
Rose Robin	-	-	-	0.20	0.05	0.25	(1)	0.12	0.17	(5)
Little Cuckoo-shrike	0.20	-	-	-	0.05	0.25	(1)	0.01	0.06	(1)
White-throated Honeyeater	-	-	-	-	-	-	-	0.66	0.76	(5)
Buff-rumped Thornbill	-	-	-	-	-	-	-	0.47	0.83	(5)

TABLE 3. Cont. Species order and abbreviations are as in Table 1.

Species	Standard surveys							Other surveys		
	Wi	Sp	Su	Au	MAF	Range	Years	MAF	Range	Years
Weebill	-	-	-	-	-	-	-	0.44	0.65	(5)
Scarlet Honeyeater	-	-	-	-	-	-	-	0.41	0.30	(5)
White-throated Treecreeper	-	-	-	-	-	-	-	0.39	0.49	(5)
Varied Sittella	-	-	-	-	-	-	-	0.30	0.43	(5)
Spotted Pardalote	-	-	-	-	-	-	-	0.23	0.23	(5)
Cicadabird	-	-	-	-	-	-	-	0.18	0.14	(5)
Jacky Winter	-	-	-	-	-	-	-	0.18	0.25	(5)
Noisy Friarbird	-	-	-	-	-	-	-	0.12	0.28	(4)
White-breasted Woodswallow	-	-	-	-	-	-	-	0.06	0.11	(3)
Rufous Songlark	-	-	-	-	-	-	-	0.05	0.18	(2)
Ground Cuckoo-shrike	-	-	-	-	-	-	-	0.03	0.12	(1)
Little Shrike-thrush	-	-	-	-	-	-	-	0.02	0.06	(2)
Dusky Woodswallow	-	-	-	-	-	-	-	0.02	0.10	(1)
Regent Bowerbird	-	-	-	-	-	-	-	0.02	0.12	(1)
Yellow-eyed Cuckoo-shrike	-	-	-	-	-	-	-	0.01	0.06	(1)
Scarlet Robin	-	-	-	-	-	-	-	0.01	0.04	(1)
Crested Shrike-tit	-	-	-	-	-	-	-	0.01	0.05	(1)
Satin Flycatcher	-	-	-	-	-	-	-	0.01	0.04	(1)
Little Grassbird	-	-	-	-	-	-	-	0.01	0.06	(1)
Brown Songlark	-	-	-	-	-	-	-	0.01	0.06	(1)
Brown Gerygone	-	-	-	-	-	-	-	0.01	0.06	(1)
Blue-faced Honeyeater	-	-	-	-	-	-	-	0.01	0.06	(1)
Fuscous Honeyeater	-	-	-	-	-	-	-	0.01	0.06	(1)
Plum-headed Finch	-	-	-	-	-	-	-	0.01	0.06	(1)
Satin Bowerbird	-	-	-	-	-	-	-	0.01	0.04	(1)

in all seasons of at least three years (i.e. MSF of 0.6 or higher). MSF values for another 25 species observed in standard surveys varied from lows of 0.0 or 0.2 to highs of 0.6 or 0.8, respectively, or higher; for eight of them minimum MSF on other surveys were always intermediate (>0.2) and, thus, only 17 species showed clear differences in seasonal presence. Another 11 species that were either missing from standard surveys, or observed at low MAF (0.2 or less) on those surveys, had minimum $MSF < 0.2$ and a range > 0.3 in other surveys, indicating that they also differed in seasonal presence. MSF in other surveys for Darter (range 0.0 to 0.28) and Black-faced Monarch (0.0 to 0.22) were consistent with those in standard surveys, confirming the small differences in seasonal presence. Approximate dates on which these 30 species with clear differences in MSF were present are shown in Fig. 2.

DISCUSSION

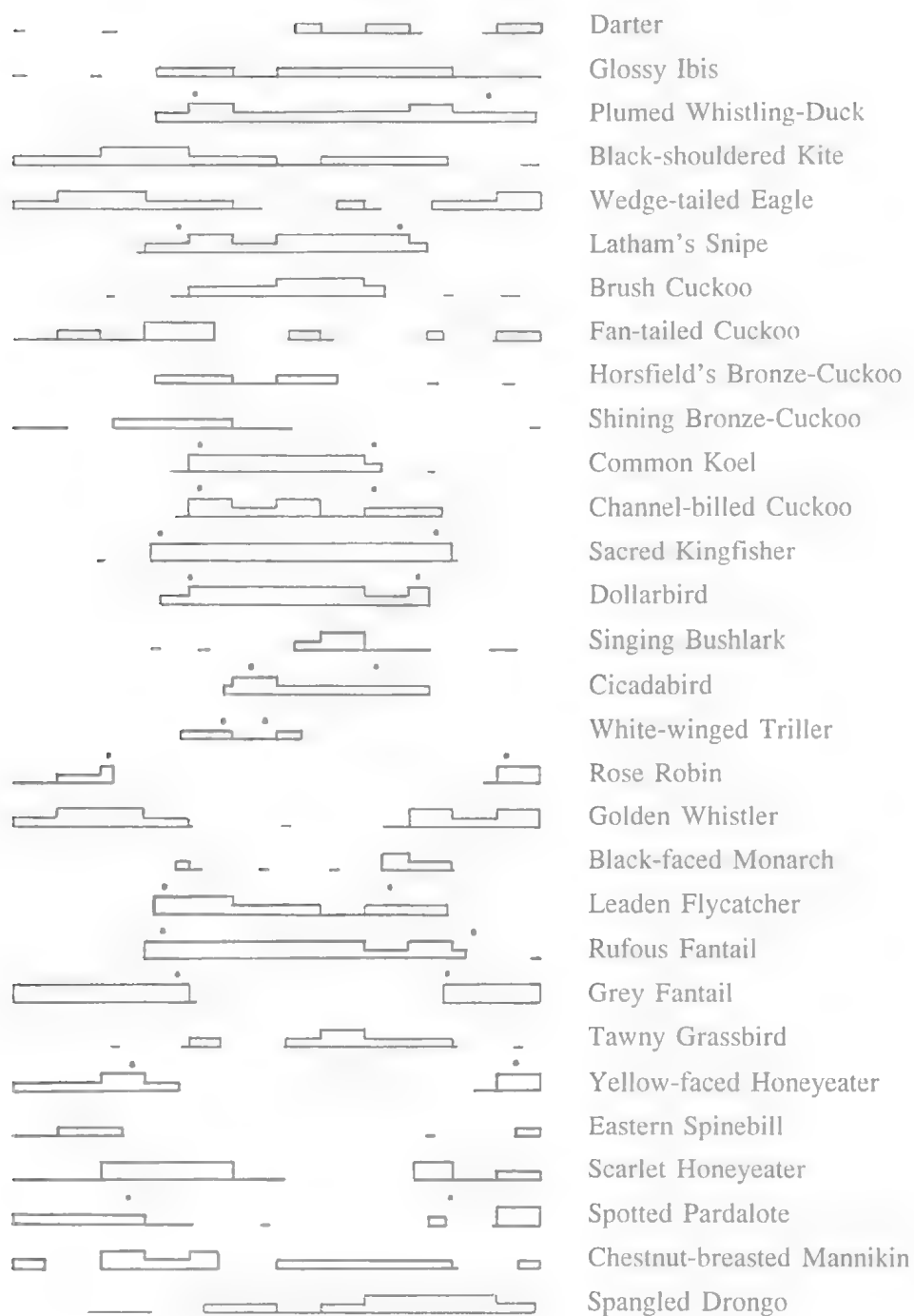
THE VALUE OF INFORMATION ON FREQUENCY OF OBSERVATION

Knowledge of ways in which abundance of bird species is influenced by land use is essential to wildlife management. For a limited range of habitats, e.g. commercial forests, this can be readily obtained in structured, systematic surveys. Such

surveys have not been done over farming landscapes, and management decisions depend substantially on opportunistic information.

The standard survey adequately monitored changes in abundance of individual species within seasons, but inferences on the relative abundance of different species, and of individual species between seasons, need to take account of differences in detectability (Emlen, 1971; Davies, 1984; Recher, 1988). Estimates of abundance also need to be based on several years of survey (Rice et al., 1983). The variable climate in Australia, particularly in southeast Queensland, makes this even more important. However, variation in frequency between years for most species in the Marburg district was low. The major exceptions were waterbirds that move nomadically in response to inland rainfall (Gosper et al., 1983; Woodall, 1985), and it is generally more useful to relate their frequency of occurrence to proximate causal factors than to determine unadjusted long-term mean frequencies. The wide variation in annual frequency for some land birds was associated with proportion of visits to a eucalypt association, reflecting restricted use of habitat in the district and the limitations of the other surveys.

Notwithstanding the preceding comments, the combination of seasonally balanced standard surveys with a larger number of other surveys pro-



J J A S O N D J F M A M

4/5 year 2/3 year 1 year

vides adequate baseline information on seasonal and annual frequency of species for habitat management. The standard surveys are repeatable, and continue, enabling long-term changes to be monitored and compared with similar information from elsewhere (e.g. the Australian Bird Count; Ambrose, 1989). Although it would be impracticable to precisely repeat the other surveys, their number and broadly specified representation of habitats ensures a useful baseline to which changes can be related.

FREQUENCY OF OBSERVATION OF SPECIES

Waterbirds. Most of the principal waterbirds observed in the Marburg district (Table 1) are widely distributed in Australia, with 17 species occurring in over 40% of 1° grid squares (Blakers et al., 1984). Those with more restricted distribution include Cattle Egret, Intermediate Egret, Plumed Whistling-Duck, Dusky Moorhen, Purple Swamphen and Latham's Snipe. In contrast, some widespread species such as Australian Pelican, Great Cormorant and Pied Cormorant were seldom observed, even though their relative frequencies were greater than 60% in annual one-day counts for the region within 80 km of Brisbane between 1972 and 1983 (Woodall, 1985). Twenty principal species were also common in northeast NSW. (Gosper, 1981; Gosper et al., 1983), with the Maned Duck the conspicuous exception.

The Marburg district, like the whole of southeast Queensland (Woodall, 1985) and northeast NSW. (Gosper, 1981; Gosper et al., 1983) is clearly rich in waterbirds. It supports many more species than regions inland of the Great Divide (Whitmore et al., 1983; Crossman & Reimer, 1986). Rural residential settlement has increased the number of dams to about 3 per km² (see Queensland Dept Mapping and Survey, Marburg Topographic Map 9442-44). Although many dams are small and lack habitat diversity (G.J. Leach, unpublished data), they supplement older, and usually larger, dams and ephemeral shallow swamps which provide more diverse habitat (Braithwaite, 1975; Leach & Hines, 1992; Wilkinson and Schwenke, 1992). Absence of major reservoirs probably restricts deep water feeders such as Australian Pelican and the large cormorants.

The range in annual frequency was generally

wider for waterbird species than for landbirds with the same MAF. Lower frequency of shoreline species in 1983-84 coincided with the end of a widespread southeast Australian drought, enabling them and birds of open water, e.g. cormorants and most ducks, to disperse inland, west of the Great Divide (Woodall, 1985; Leach & Hines, 1992). In contrast higher annual frequencies for several species occurred in the drier 1980-81 and 1982-83 years.

Non-passerine landbirds. Eleven of the principal non-passerine landbirds (Table 2) are widely distributed in Australia and the remaining 10 species occur in at least 11% of 1° grid squares (Blakers et al., 1984). Among the most frequently observed, Spotted Turtle-Dove, Peaceful Dove and Cockatiel were better represented at Marburg than in surrounding districts.

The principal species are birds of open country, the 'edge' between woody vegetation and open country, or farmlands. Few were numerous and five with a MAF of 0.5 or higher were ground-feeding pigeons and three were parrots. The Feral Pigeon, Spotted Turtle-Dove, Crested Pigeon and Galah were commensal with farming, and their abundance probably reflects the intensity of small-scale cropping, whereas the Peaceful Dove and Bar-shouldered Dove appear to depend on softwood scrub remnants. Among remaining species with MAF of 0.5 or higher, Australian Kestrel and Rainbow Bee-eater hunt over open country and contrast with Scaly-breasted Lorikeet, Pale-headed Rosella and Laughing Kookaburra utilising open-forest/woodland and the Pheasant Coucal using dense scrub and/or rank grass. Sacred Kingfisher was the only species with MAF > 0.5 in other surveys that had MAF < 0.5 in standard surveys, probably reflecting its preference for the open eucalypt forest with many termitaria for nest sites.

The most notable feature of the non-passerine landbirds was that half of them were observed on 5% or fewer visits, yet none are rare in southeast Queensland (Roberts, 1979). They included several raptors and parrots. The group also included the fruit-doves usually associated with closed-forest or softwood scrub, even though the district has many, isolated, *Ficus* spp. which produce heavy crops of fruit (Leach & Hines, 1987). The remnants of low closed-forest may be too small, too degraded, too isolated from extensive rainfor-

FIG. 2. Periods when species with substantial differences in MSE (see text) were present. Continuous lines/block-join observations at closer than 4-week intervals, based on combined observations over 5 years. Number of years when species were present in each month and single observations are shown. Mean dates of arrival and departure of strongly seasonal migrants are also shown (●).

TABLE 4. The numbers of principal and non-principal species in standard surveys, and of species observed only in other surveys, classed according to low, medium and high variation in annual frequency. For standard surveys low, medium and high variation are represented by values of 0.0 or 0.25, 0.5, and 0.75 or 1.0 respectively; for other surveys the corresponding values are ≤ 0.25 , 0.26 to 0.5, and > 0.5 respectively. The numbers of species with MAF ≤ 0.20 in other surveys are shown in parentheses.

Range in annual frequency		Water-birds	Non-Passerines landbirds	Passerines	Total
Standard surveys	Other surveys				
Principal species					
Low	Low	6	6	20 (1)	32 (1)
"	Medium	5	4	4	13
"	High	2	0	1	3
Medium	Low	1	7 (1)	5 (1)	13 (2)
"	Medium	1	2	7	10
"	High	2	0	2	4
High	Low	0	0	2	2
"	Medium	6	2 (1)	4	12 (1)
"	High	1	0	1	2
Sub-total		24	21 (2)	46 (2)	91 (4)
Non-principal species					
Low	Low	3 (3)	11 (10)	6 (5)	20 (18)
"	Medium	0	4 (2)	4 (2)	8 (4)
"	High	2 (1)	0	2	4 (1)
Medium	Low	2 (2)	2 (2)	1 (1)	5 (5)
"	Medium	0	0	2 (2)	2 (2)
"	High	0	0	0	0
High	Low	0	0	0	0
"	Medium	1 (1)	0	0	1 (1)
"	High	0	0	0	0
Sub-total		8 (7)	17 (14)	15 (10)	40 (31)
Species observed on only the other surveys					
—	Low	10 (10)	21 (20)	20 (19)	51 (49)
—	Medium	1 (1)	1 (1)	4 (1)	6 (3)
—	High	1 (1)	0	3	4 (1)
Sub-total		12 (12)	22 (21)	27 (20)	61 (53)
Total		44 (19)	60 (37)	88 (32)	192 (88)

est and/or naturally floristically unsuitable for other than limited opportunistic exploitation by fruit-doves. Fruit-doves were only occasionally observed immediately following European settlement at Murphy's Creek, 50km west (Lord, 1956), but whether they were more prominent in the more extensive softwood scrub of the Marburg District (Elsol, 1991) cannot be ascertained.

Passerines. Twenty-three principal passerines (Table 3) have a wide Australian distribution, while five were reported from $< 11\%$ of 1° grid squares (Blakers et al., 1984). The latter include species associated with closed-forest (Varied Triller, Eastern Whipbird and Lewin's Hon-

eyeater) or rank grassland (Tawny Grassbird) and the Common Myna. Nine species with low MAF (0.2 or less) (Tree Martin, White-winged Triller, Jacky Winter, Restless Flycatcher, Rufous Songlark, Brown Songlark, Weebill, Varied Sittella and White-breasted Woodswallow) are widely distributed in Australia. Nine non-principal species are restricted to $< 11\%$ of the Australian 1° grid squares, with Yellow-eyed Cuckoo-shrike, Black-faced Monarch, Little Cuckoo-shrike, Brown Gerygone, Satin Bowerbird and Regent Bowerbird associated with closed-forest. Species observed more frequently than in neighbouring grid squares include Grey-

crowned Babbler, Superb Fairy-wren, Yellow Thornbill, Speckled Warbler, Striped Honeyeater and Zebra Finch.

Passerines are clearly the most important component of the avifauna, both in terms of species number (Leach & Hines, 1987) and frequency of observation (Table 3). Thirty-three of the species listed in Table 3 were observed in roadside remnant vegetation in summer, including 31 principal species (Leach & Recher, 1993). The six most numerous species in roadside remnants, namely Silvereye, Superb Fairy-wren, Yellow Thornbill, Double-barred Finch, Red-backed Fairy-wren and Lewin's Honeyeater had MAF of 0.75 or more.

Cicadabird, Weebill, White-throated Gerygone, Buff-rumped Thornbill, Varied Sittella, White-throated Treecreeper, White-throated Honeyeater and Spotted Pardalote, with much higher MAF in other surveys than in standard surveys, are largely restricted to the eucalypt associations (G.J. Leach, unpublished data), corroborated by correlation of their MAF with proportion of visits to eucalypt stands at Tallagalla. Other differences in MAF between surveys also reflect the proportion of visits to eucalypt associations, e.g. Yellow-faced Honeyeater and Pied Currawong.

Among species with greater MAF in standard surveys than in other surveys, the narrow range in annual frequencies for Singing Bushlark, Tawny Grassbird and Yellow-rumped Thornbill confirms their localised distribution. This reflects preference for open country, rank grassland, and close-grazed or mown grassland around isolated trees, respectively (Leach & Hines, 1987). Larger ranges in annual frequency contribute to the difference in MAF between surveys for Fairy Martin, Richard's Pipit and Red-backed Fairy-wren, but at least part of the difference for the first two is likely to reflect preference for open habitat. The difference for the Red-backed Fairy-wren may be related to its abundance in roadside vegetation (Leach & Recher, 1993) and use of swamp grasslands (Leach & Hines, 1987).

The introduced Common Myna colonized the district from the west during this survey, reaching the eastern boundary in 1982 (Leach & Hines, 1987). Correlations with visits to Woolshed Creek Road and Prenzlau, in the west, probably reflect marginally longer colonization in these areas.

A wide range of families and feeding strategies are represented among principal passerines. Approximately half the species primarily use open,

or disturbed, habitats (Schodde & Tidemann, 1986). Exceptions associated with closed-forest/softwood scrub include Varied Triller, Grey Shrike-thrush, Rufous Fantail, Eastern Whipbird, White-browed Scrubwren, Yellow Thornbill, Silvereye, Lewin's Honeyeater and Figbird (Howe, 1986; Leach & Recher, 1993).

Species using rainforest patches in northern NSW were grouped according to size of patch occupied (Howe, 1986). The first 21 species listed in Table 3 were not in the more specialised rainforest groups. The Rufous Fantail and White-throated Treecreeper were placed in a group requiring patches larger than 2.5 ha. However, the Rufous Fantail was common in narrow roadside remnants at Marburg (Leach & Recher, 1993), whereas the White-throated Treecreeper was mainly observed in open eucalypt forest on other surveys. Several species occurring in small and large rainforest patches, but predominantly the latter, were observed in roadside remnants at Marburg, indicating that habitat use differs from that in northern NSW. An explanation for the differences may be that abundant *Lantana camara* and other woody weeds provide a more effective linkage between small remnant patches for many bird species than in northern NSW (Lynch, 1987; Lynch & Saunders, 1991; McIntyre & Barrett, 1992; Leach & Recher, 1993). Because the diversity and abundance of passerines may be more vulnerable to intensified land use than their current status indicates (cf. Recher & Lim, 1990), it may become especially important to retain, and where possible regenerate, native woody vegetation if woody weeds are substantially controlled and cleared.

SEASONAL MIGRANTS

Surveys were sufficiently frequent to provide approximate dates of arrival and departure of migrant species (Fig 2). Some species are clearly summer (e.g. Latham's Snipe, Common Koel, Leaden Flycatcher and Rufous Fantail) or winter (e.g. Rose Robin, Grey Fantail and Yellow-faced Honeyeater) visitors, with little variation between years in dates of first or last observation. Some tended to be absent from the district for only a very short period (e.g. Black-shouldered Kite and Wedge-tailed Eagle) while White-winged Triller was present for only a short period. Others (e.g. Scarlet Honeyeater and Spotted Pardalote) were consistently observed at disjunct intervals. Several migrants consistently arrived in late September, e.g. Common Koel and Dollarbird, but dates of last observation were more variable.

Information for southeast Queensland, mainly limited to honeyeaters at Wellington Point (Robertson, 1958, 1965; Robertson & Woodall, 1983), is significantly augmented. Features of special interest are the small period of overlap between the Rufous Fantail and the Grey Fantail in September and March/early April, the short winter presence of the Rose Robin, the short visit of the White-winged Triller for breeding (G.J. Leach, unpublished data), and migration patterns in the honeyeaters. Low MSF in summer and/or autumn for some otherwise relatively common raptors indicates that further study is necessary to establish if this is the result of seasonal movement, or is associated with behavioural changes that affect detectability while breeding. Latham's Snipe is the only truly seasonal migrant among the principal waterbirds because Plumed Whistling-Duck is a winter resident in the neighbouring grid square (Leach & Hines, 1987). Information for other waterbirds, e.g. Black Swan and Glossy Ibis, reflects nomadic movements.

Summer presence of the Rufous Fantail in the Marburg district agrees with observations in northeast NSW. (Cameron, 1985). However, the Grey Fantail was more numerous in summer than winter in NSW. Roberts (1979) remarks that Grey Fantails are resident in southeast Queensland with an increase in numbers in winter. Our data shows that it is not resident in all habitats, possibly because different races may occupy different habitats (Cameron, 1985). Mist netting since 1988 has shown that small numbers of both species are present outside the dates in Fig. 2 (G. R. Anderson & G.J. Leach, unpublished data), suggesting that more monitoring of their movements is necessary.

Observations for the Yellow-faced Honeyeater and Eastern Spinebill (Fig. 2) closely match those of Robertson and Woodall (1983). The continuous presence of Scarlet Honeyeaters at Wellington Point from March through September contrasts with its frequent absence through mid-winter in the Marburg district where it, and also the Spotted Pardalote, appear to be seasonal migrants responding to local variation in availability of food.

CONCLUSIONS

The Marburg district supports a rich diversity of bird species, with waterbirds and passerines generally better represented than non-passerine landbirds. The diversity is sustained by the wetlands, remnants of brigalow softwood scrub, eu-

calypt open-forest and the woody weeds interspersed through the farmlands. The survey has established a robust database which will allow changes in mean annual and seasonal frequency of bird species to be detected. The information should be used to guide management of these diverse habitats.

While the avifauna (with the exception of most non-passerine landbirds) is well-adapted to the existing matrix of terrestrial and wetland habitats, additional human settlement and intensification of land use may lead to a breakdown of this matrix. Regular monitoring is vital. Maintenance of the present diversity and abundance of birds will require management strategies aimed at retention and better management of existing native woody vegetation, and re-vegetation with appropriate native species wherever practicable.

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APPENDIX 1 Details of localities in the standard survey which were surveyed on foot.

Location	Grid Ref.	Duration (mins)	Habitats			
			Roadside	Paddocks	Dams	Other
Haigslea (School)	MQ631500	45	T(1,A,B), G(s-r).	T(1,A), G(s), C(1).	M1, M2 & M3 (s) + 1(s, silted with <i>Typha</i> sp. and adjacent <i>Schinus terebinthifolia</i>).	School and church grounds. T(2, native & exotic), G(s).
Haigslea	MQ618495	20	G(r).	T(1,A), G(r), C(1).	M4(m) + 1(m).	
MT Marrow	MQ627481	20	T(2,S,A), W(2,L), G(r).	T(2,S,A), W(2,L), G(s-r).	M5(s).	Road metal quarry south of road.
Malabar	MQ609483	15	T(1,A), W(1,C,L), G(r).	T(1,A,B), W(1,L,C), G(m-r).	M6(1).	
Malabar	MQ609477	30	T(2,S,A,B), W(2,L), G(r).	T(1,S,A), W(1,L), G(m-s).		Dis-used sand quarry south of road. Cliffs used by hole-nesting species (see Leach and Hines, 1987).
Tallegalla (Railway dam)	MQ577467	10	T(1,A), W(1,C,L), G(m-r).	T(1,A,B), W(1,L), G(s).	1(m, covered with Water hyacinth, <i>Eichhornia crassipes</i>).	
Tallegalla (The Bluff)	MQ550464	30	T(2,S,A), W(2,L), G(m-r).	T(2,S,A), W(2,L), G(s-m).	2(s, often empty)	Three large <i>Ficus</i> spp. at this site.
Ashwell	MQ561446	20	T(2,S,A,B), W(2,L), G(r).	T(S,B,E,A), W(2,L), G(s-r).		Small creek through site
Minden Dam	MQ548522	15	T(1,A,S), G(s-r).	T(2,E,B,S), G(s-r).	1(m - Leach & Hines, 1992).	Mid-afternoon.

1. Grid References for Marburg (9442-44) and Haigslea (9442-41) 1:25 000 Topographic Maps.
 2. Vegetation:
 T - trees; 2, 1 - more than 5, and 1 to 5, respectively >8m tall in vicinity. Principal trees are Brigalow (*Acacia harpophylla*) (B), other acacia spp. (A), softwood species (S, see Leach & Hines, 1987), and eucalypts (E).
 W - woody weeds; 2 - extensive thickets, 1 - isolated clumps; species include lantana (*Lantana camara*) (L) and Wait-a-while (*Caesalpinia decapetala*) (C).
 G - grass; s - grazed short, m - medium grazed to about 500mm tall, r - rank, often not grazed and over 1000mm tall.
 C - cultivated land nearby, <20% of total area within 500m of road.
 Additional details of roadside vegetation on parts of the standard route are in Leach & Recher (1993).
 3. Dams - those prefixed 'M' are described in Leach (1994). Minden is described in Leach & Hines (1992).
 Dams are described as large (l, >15 000m² maximum surface area), medium (m, 5000 to 15 000m²) or small (s, <5000m²).

APPENDIX 2 Principal areas visited in the 100 non-standard surveys.

Locality	Number of visits	Habitats	Remarks
Haigslea/Malabar/MT Marrow.	92 ¹	As first five sites on standard route, plus extra softwood remnants.	82 to 100% of visits each year.
Schumans Road.	71 ⁴	Well-conserved lengths of softwood scrub gallery, about 7m wide (Leach & Recher, 1993).	24% of visits in 1980-81; 68 to 100% thereafter.
The Bluff, Tallegalla	19	See App.1.	10 to 29% of visits each year.
Woolshed Creek Road - East.	83 ²	Lengths of softwood scrub gallery, about 8m wide plus small creek and gallery of <i>Melaleuca bracteata</i> .	65% of visits in 1980-81, progressively increasing to 100% in 1984-85.
Woolshed Creek Road - West.	78 ²	Eucalyptus open-forest (especially <i>E. maculata</i>) with woody weeds and grazed grass understorey (Leach & Hines, 1987).	47% of visits in 1980-81, increasing through 69, 84, 90 and 100% in following years.
Glamorgan Vale - MT Stradbroke.	9	As Haigslea/Malabar/MT Marrow, plus more extensive areas of relatively intact Brigalow-softwood scrub.	29% of visits in 1980-81, 15% in 1981-82, none subsequently.
Prenzlau Swamp ³ .	36	Shallow ephemeral swamp (Leach & Hines, 1987).	First visited in March 1981; 18% of visits in 1980-81, increasing through 23, 32, 40 and 72% in following years.

(1) Censuses of farm dams (Dams M1 to M6, see Appendix 1) were major objectives on 14 of these visits.
 (2) Transect censuses carried out on 12 of these days and rolling bird surveys (Cullen, 1980) on another 40 days. Five rolling bird surveys were completed in spring and autumn of each of the last four years, substantially contributing to the discrepancy in number of visits between seasons.
 (3) Prenzlau Swamp. Extensive open water (c.100ha) in March 1981, reduced by 80% by October 1981 and almost no open water by October 1982. Flooded in May 1983 and extensive open water thereafter apart from early summer 1984-85.

CRAB ISLAND REVISITED: REASSESSMENT OF THE WORLD'S LARGEST FLATBACK TURTLE ROOKERY AFTER TWELVE YEARS

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Limpus, C.J., Couper, P.J. & Couper, K.L.D. 1993 06.30: Crab Island revisited: reassessment of the world's largest Flatback Turtle rookery after twelve years. *Memoirs of the Queensland Museum* 33(1):277-289. Brisbane. ISSN 0079-8835.

Crab Island in northeastern Gulf of Carpentaria supports the largest nesting population of *Natator depressus*, a marine turtle endemic to the Australian continental shelf, and low density nesting by *Eretmochelys imbricata*. The reproductive status of the Flatback Turtle, *Natator depressus*, at Crab Island, is reassessed after 12 years based on a survey conducted during high density nesting in July 1991. *N. depressus* hatchling productivity from the island continues to be high. The characteristic small size of nesting females and egg diameters of *N. depressus* that breed in the Crab Island region suggests that this population is a different breeding unit from that of the southern Great Barrier Reef. The feeding areas supplying turtles to the Crab Island region rookeries extend as far north as southern Irian Jaya. □ *Natator depressus*, *Eretmochelys imbricata*, Crab Island, Queensland, Australia, nesting, hatchling productivity, conservation status.

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Crab Island, in the north eastern Gulf of Carpentaria, supports the largest recorded nesting aggregation of Flatback Turtles, *Natator depressus* (Limpus & Parmenter, 1986). *N. depressus* is almost totally confined to the Australian continental shelf and its breeding is restricted to Australia (Limpus et al. 1988). The biology of marine turtle populations breeding on Crab Island was reviewed by Limpus et al. (1983a) based on field surveys of the nesting turtles in 1970-1979. Because the status of this significant turtle breeding population had not been reassessed since that time, a study to redescribe the reproductive biology of the Crab Island turtles after a 12 year interval was undertaken in July 1991, during the high density nesting period identified in previous studies (Limpus et al. 1983a).

METHODS

A two person team camped on Crab Island during 6-22 July 1991 (P.J.C. and K.L.D.C.). The western (ocean) beach of the island was measured along the spring high tide level and subdivided into eleven numbered sectors (each 500m long) from south to north (Fig. 1) using a pedometer. All data recorded along the island were scored by beach sector. The beach width within sectors 1-10 was measured from the spring high tide level to the crest of the seaward dune adjacent at each sector mark. These were the sectors in which all turtle nesting activity occurred. On arrival, the

team counted all existing turtle tracks by species, without attempting to age the tracks. A single track included both the emergence and return crawl of a nesting turtle. All tracks were crossed off in the sand above the high tide mark as they were counted so that previously recorded tracks could be recognised. Thereafter, a track census was conducted daily: all turtle tracks and nests from which hatchlings had emerged from the previous night were counted by species along the western beach. Because two persons could not monitor the nesting behaviour of all turtles ashore for a night along 6km of beach, a subset of the beach sectors (4 to 6) was selected for nightly measurement of nesting success of each turtle. Potential predators of the turtles, their eggs or hatchlings were identified and quantified where possible. This included counting of crocodile and bird tracks. Turtles were recorded in the waters adjacent to the nesting beach during the daily census of tracks on those days when the weather was relatively calm. As well, a male turtle was captured by 'beach jumping' (cf. Limpus & Reed, 1985).

Opportunistic tagging of nesting female turtles occurred when volunteer members of the Queensland Turtle Research Project visited Crab Island (28 December 1989 and 15-17 January, 1991) and the south beach at the mouth of the Jardine River on the mainland, 14km from Crab Island (29 December 1987). Adult turtles were tagged using

serially numbered, self piercing, self locking tags applied to the axillary flipper tagging position (Limpus & Reed, 1985). In July 1991, 3.3g monel tags (National Band and Tag Company, style 1005, size 681; SD = 0.01g, range = 3.25-3.29, n = 50), inscribed with a return address on the reverse side (Ecology, Box 26 Woden 2606 Australia), were used. On the other visits, 4.1g titanium turtle tags (Stockbrands Co. P/L., return address: Wildlife Box 155 North Quay 4002 Qld Australia; Limpus, 1992) were used. The turtles were double tagged, one tag in each front flipper. No attempt was made to tag all turtles ashore in any one night. The measurements taken followed the standard methodology of the Queensland Turtle Research Project as described by Limpus et al. (1983a): midline curved carapace length (CCL); clutch count; egg diameter, egg weight (10 eggs randomly selected per clutch); nest depth to the bottom of the egg chamber; incubation and emergence success of clutches; sand temperature at 50cm depth. Samples of eggs and recently dead hatchlings were collected and deposited in the Queensland Museum.

Air temperature, rainfall and wind data have been obtained from the Bureau of Meteorology (Brisbane) for their weather station at Thursday Island (10°35'S, 142°13'E, 60m elevation, 45km from Crab Island). This is the closest weather station to Crab Island for which there is a comprehensive data set. Tidal data for Booby Island was used (Anon, 1990). Booby Island, 47km to the north west is the closest standard port tidal bench mark across open water to Crab Island.

RESULTS

STUDY SITE

Crab Island (10°59'S, 142°06'E, Fig. 1) is a crescentic sand island that measured 6.2km in length along the high tide level of the outer western beach on 6 July. The inner eastern margin of the island was partly mangrove lined with wide inter-tidal mud flats. The western beach was composed of mixed siliceous sand and calcium carbonate (broken mollusc) fragments and was exposed to surf. Beach rock was exposed intertidally in sectors 4 and 5. The vegetation of the foredune nesting habitat of the western beach was variable; *Melaleuca* woodland with a grass and herb understorey in sectors 5 and 6; open woodland of scattered *Casuarina equisetifolia* (sectors 4 and 7); grassland dominated by *Spinifex hirsutus*, *Ipomoea pes-caprae* and *Tribulus cistoides* (sectors 2-4, 5, 8-10); unvegetated sand dune

(sector 6). There were no mangroves growing on the western beach. However, there were standing dead mangrove trunks on the northern part of the western beach that were the result of past encroachment of the island into the mangrove forest. The dead mangroves and beach rock were not an impediment to the nesting activities of the turtles.

Crab Island lies within a region with a distinct summer wet season and winter dry season. The mean monthly rainfall and the mean daily minimum and maximum temperatures for the years 1950-1991 at Thursday Island ranged from 4mm in September to 419mm in January (Fig. 2). Crab Island has no surface freshwater for most of the year. There is an ephemeral freshwater swamp system behind the dune in the northern end of sector 5 which supports at least one species of frog, *Limnodynastes ornatus* (QMJ31755-7). This swamp was dry during the July visit and in most years there would be insufficient rain to refill the swamp until January, which is the peak of the wet season (Fig. 2). Monthly mean daily maximum temperatures ranged from 31.2°C in November to 27.7°C in July, while monthly mean daily minimum temperatures ranged from 25.4°C in December to 22.5°C in July. During the middle of wet season months of January and February the wind is predominantly from the west and north-west and is mostly weaker than 20km/hr. In the middle of dry season months of May to October there are almost no westerly or northwesterly winds; the dry season winds come predominantly

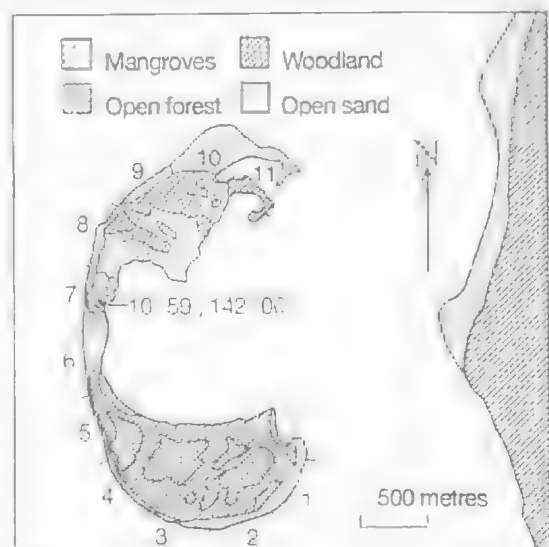


FIG. 1. Map of Crab Island showing position of numbered beach sectors and vegetation types.

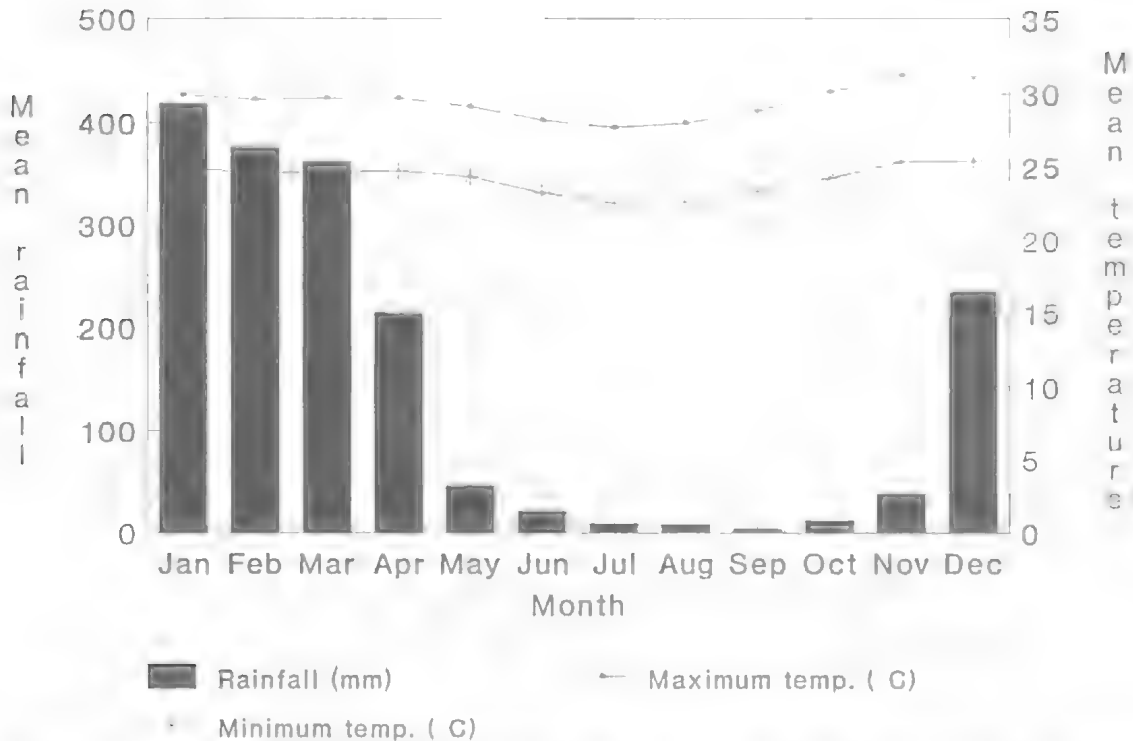


FIG. 2. Monthly mean rainfall (mm) and monthly mean daily minimum and maximum temperatures recorded at Thursday Island Meteorological Station for the years 1950-1991.

from the east and southeast and are mostly stronger than 20km/hr. Mean sand temperature at 50cm depth within the turtle nesting habitat was 27.6°C (SD = 0.49, range = 26.4 - 28.5, $n = 44$, 1 - 5 measurements per night).

The mean beach width above the spring high tide level was 31.3m (SD = 15.3, $n = 10$). The narrowest beach (8m) occurred at sector mark 3 and the widest (53m) at sector mark 10. There are two high tides per 24hr at Crab Island (Fig. 3). During 6-22 July, 1991, the daily tidal range varied from 3.46m (12th) to 2.36m (19th). The variation in night time high tide height (0.27m) was less than that of the daytime high tides and both sets of low tides (Fig. 3).

NESTING TURTLES

On the team's arrival at the island on 6 July, 1991, there were 309 turtle tracks visible (174 *N. depressus*, 135 not identifiable to species). Based on nightly track counts from the 14 nights 6-19 July (Fig. 3), there was an average of 132.7 beachings of *N. depressus* per night (SD = 52.11, $n = 14$, range = 68-235) from a total of 1839 recorded beachings. Similarly, there was an average of 0.6

beachings of *E. imbricata* per night (SD = 0.93, $n = 14$, range = 0-3) for a total of 9 beachings.

On the limited data from this visit, there is a suggestion that the maximum nightly nesting density may follow the occurrence of afternoon high tides. Only *N. depressus* was recorded coming ashore for nesting during daylight hours (19 [1.0%] of the 1839 total beachings). Most (4 and 13) of these daylight nesting emergences occurred on two days only (8th and 9th July, respectively) with the remainder being single beachings on each of the 10th and 20th July. All except one of the daylight beachings occurred on days with mid-afternoon high tides (8th-10th) while the remainder coincided with a midday high tide (20th).

Turtle nesting activity was restricted to the western (ocean) beach, except for one turtle which came ashore on the western side at the narrow middle of the island (sector 6) and returned to the sea on the eastern side. Most nesting activity occurred within the middle sectors 4-8 (Fig. 4) where the beach width ranged 26-43m. The number of turtle beachings varied nightly and among sectors. The densest activity occurred in sector 5 (nightly mean number of tracks = 43.9,

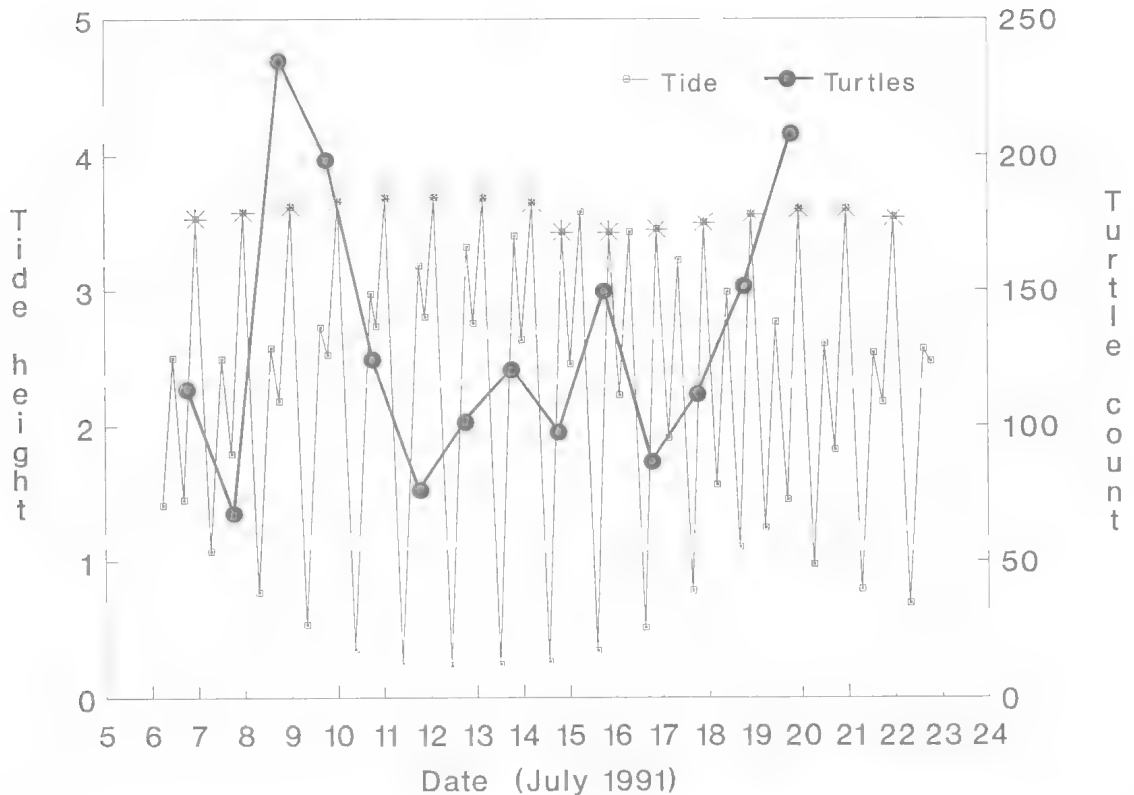


FIG. 3. Daily frequency of beachings by nesting Flatback Turtles, *Natator depressus*, at Crab Island during 6-19 July 1991. The daily variation in tide height (in metres), measured at Booby Island is also shown. *denotes a night time high tide.

SD = 25.49, $n = 14$, range = 21 - 102) while no tracks were recorded on any night in sector 11.

For the sample of 172 beachings by *N. depressus* examined for nesting success, 132 females (76.7%) definitely laid eggs, 14 (8.1%) could not be determined for nesting success and 26 (15.2%) returned to the sea without laying eggs. Thus there was a probability ($\pm 95\%$ confidence limits) of between $76.7 \pm 3.2\%$ and $84.8 \pm 2.8\%$ that a turtle would successfully lay eggs when she came ashore. When this nesting success probability is applied to the track counts for the period 6-19 July, it is estimated that between 1352 and 1611 *N. depressus* clutches were laid on the island during the 14 nights of observation.

For the sample of 6 beachings by *E. imbricata* examined for nesting success during the same period, 4 laid and 2 did not lay. This represents a nesting success of 67% for this species with an estimated total of 7 clutches laid during the 9 beachings.

Over the 15 nights, 6-20 July, 489 nesting turtles were examined and tagged (483 *N. depressus*

and 6 *E. imbricata*). There were no recaptures of any turtles that had been tagged during previous visits to the island, nor were there migrant recaptures of any turtles tagged at other locations. The size distribution of these nesting turtles are summarised in Table 1 and Fig. 5. The mean CCL of the nesting turtles was: *N. depressus* = 88.2 cm, *E. imbricata* = 83.9 cm.

TURTLES ADJACENT TO BEACH

By day when the weather was calm during 6-21 July 1991, there were numerous sightings of solitary turtles surfacing to breathe, mostly within 50m of the beach. All were adult sized *N. depressus*. Up to 15 such turtles were observed adjacent to a single sector during a track census with 0-49 isolated turtles seen during a single track census along the entire beach. The water was clear enough at high tide for adult sized *N. depressus* resting on the bottom at 2m depth to be visible from a dingy adjacent to the beach. In addition, mating turtles were observed in the surf adjacent to the beach on four days (0-2 courting pairs per

TABLE 1. Curved carapace length (cm) of nesting female turtles on Crab Island and adjacent beaches since the studies of Limpus et al. (1983a).

Species	Location	Date	Mean	SD	range	n
<i>Natator depressus</i>	Crab Island	15-16 Jan 1991	90.3	2.49	85.0-95.5	18
		06-20 Jul 1991	88.2	2.80	77.0-95.6	315
	mouth of Jardine River	29 Dec 1987	88.8	0.47	88.5-89.5	3
<i>Eretmochelys imbricata</i>	Crab Island	28 Dec 1989	86.0	—	—	1
		06-20 Jul 1991	83.9	2.41	79.5-86.5	6

daily track census). All were mounted pairs of *N. depressus* and no attendant males were observed. One mounted male (B0314) was captured and measured: CCL = 83.1cm, tail length beyond the carapace = 22.0cm (Fig. 6). The adult male *N. depressus* was similar to the adult female (Fig. 7) in most external features: colour, low doming of the carapace along the midline and lateral upwards reflexing of the carapace (Limpus et al., 1988). The only observed external dimorphic characters were tail length (male very long vs female short) and claws (male elongate and strongly recurved vs female short and slightly curved). The male was mounted on the female,

venter to dorsum (Fig. 8), and was gripping the female's carapace margin via the single recurved claw on each flipper. The male was mounted well forward on the female such that his head could rest on her anterior carapace and dorsal neck. His snout contacted her head when she raised her head for a breath.

ADULT MORTALITY, INJURIES AND DISEASES

No dead turtles were found along the beach on arrival on 6 July. The highest and narrowest dunes on the island were in sector 4. The 10m high dune front in this area was steep enough for most turtles to have difficulty in climbing it. One female *N.*

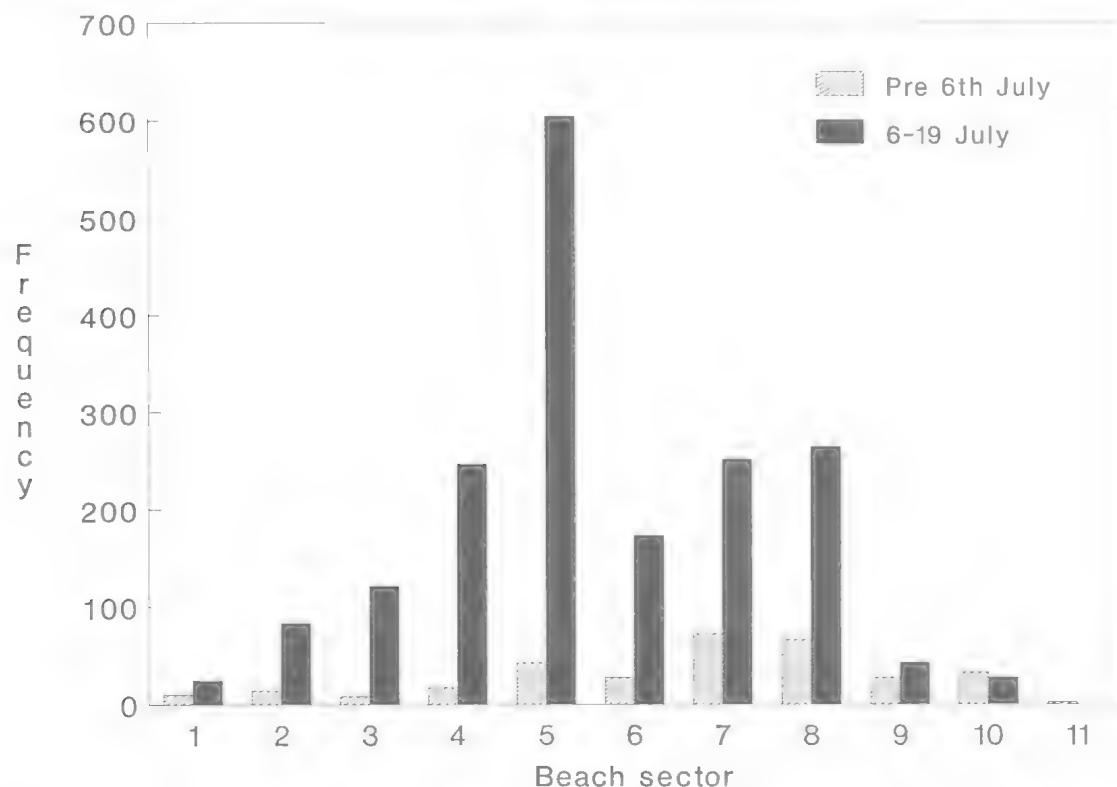


FIG. 4. Distribution of turtle tracks by beach sector on Crab Island, 6-19 July 1991.

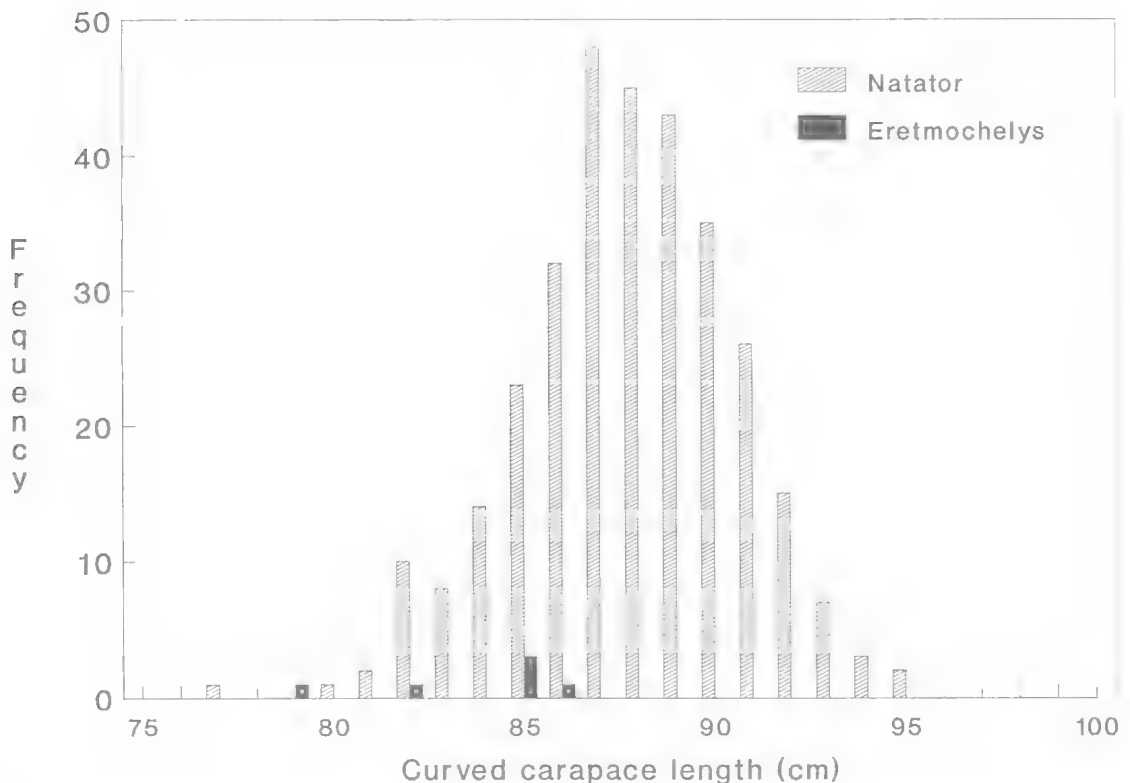


FIG. 5. Size distribution of nesting female *Natator depressus* and *Eretmochelys imbricata* at Crab Island, 6-20 July 1991.

depressus was observed to climb this dune and attempt to nest inland of the dune crest. Later, after wandering to the inland base of these dunes, she was able to find her way back to the beach and return to the sea. A search of the woodland and forest areas inland of the dune crest throughout the island revealed the old fragmented skeletal remains of two adult sized *N. depressus* lying ventral side down behind sector 4. These remains were consistent with the turtles having died after being disoriented following a nesting attempt inland of the crest of the high dunes. No nesting females died while ashore during the 6-21 July 1992 visit.

One large crocodile, *Crocodylus porosus*, (total length 3+m) was observed on most days during late mornings at the water's edge in sector 3. While this crocodile was large enough to be a predator of adult turtles, no turtles showed signs of having been mauled by a crocodile. Several nesting turtles did, however, have healed crescentic damage to the carapace that was presumed to have resulted from past shark or fish bites. For *N. depressus*, loss of large crescentic pieces from the

carapace was recorded for 8 (1.7%) turtles, minor carapace damage was recorded for 17 (3.5%) turtles and loss of one third or greater of a flipper was recorded for 32 (6.6%) turtles. All of these injuries were from well before the current nesting season as indicated by their completely healed state. None of the *E. imbricata* showed signs of significant injuries.

Fibropapillomas were recorded on five of the nesting *N. depressus* only: B505, 2 fibropapillomas on neck; B535, 2 on right hind flipper; B625, 1 on right front flipper; B690, 1 on the right shoulder; B1165, 1 on neck. The largest fibropapilloma was 2.4cm in diameter. The ventral surface was not examined.

CLUTCHES

For *N. depressus*, the mean clutch count was 55.9 eggs (Table 2, Fig. 9) and the mean egg diameter was 4.93cm (Table 2). Of the 32 clutches counted at oviposition, one contained one yolkless egg and none contained multiyolked eggs. During the laying of these 32 clutches the



FIG. 6. Adult male *Natator depressus*, tag number 80314, returning to the sea after being brought ashore for tagging and measurement.

nesting females did not dig into any existing clutches.

For *E. imbricata*, the mean clutch count was 139.3, the mean egg diameter was 3.60 cm and the mean egg weight was 26.1 g (Table 2). None of the four clutches counted at oviposition contained yolkless or multiyolked eggs. During none of the five successful nestings observed did the turtle dig into an existing clutch.

Representative eggs were collected: 6 normal *N. depressus* eggs, QMJ31745; 1 yolkless *N. depressus* egg, QMJ31747; 3 normal *E. imbricata* eggs, QMJ31746.

EMERGED CLUTCHES

Eighty four freshly emerged clutches were identified to species by examination of eggs, hatchlings or hatchling tracks. All were *N. depressus* clutches. Representative hatchling *N. depressus* were collected: QMJ31748-31753. Strong winds prevented the accurate count of emerged clutches for all beach sectors on most nights. Within the relatively wind protected area of sector 5, the nightly number of emerged clutches was counted on 6-15 July. The mean number of *N. depressus* clutches emerging per night in this sector was 4.1 (SD = 2.23, range = 0-8, $n = 14$ nights, 57 nests). The maximum number of emerged clutches counted along the entire beach on a night with light wind was seven, with four of those in sector five. Hatchlings were often encountered crossing the beach at night but none were seen by day.

Forty nests from recently emerged clutches were dug to assess hatchling incubation and emergence success. After having been laid, two of these clutches had been each dug into by another turtle, representing a clutch disturbance rate after having been laid of 0.05. Another of these

40 emerged clutches had been laid by a turtle that had dug into an existing clutch (clutch disturbance rate at laying = 0.025). Because these latter eggs were adjacent to another previously emerged clutch they could not be counted accurately. Counts were made from the remaining 39 freshly emerged clutches (Table 3). There was no significant difference (t test, $p < 0.05$) between mean clutch count measured at laying (Table 2) and mean clutch count measured at emergence (Table 3, Fig. 9), the latter having been laid approximately two months earlier. The mean depth to the bottom of these nests was 58.3 cm (Table 3). There were yolkless eggs (1 per clutch) in two of these clutches.

From the 2129 eggs in the 39 clutches counted, there was a mean hatching success of 81.84%, while hatchling emergence from the nest to the beach surface represented 78.56% of the eggs laid (Table 3). Egg mortality was distributed as follows: 10.4% unhatched, 7.4% undeveloped and 0.3% predation by ghost crabs, *Ocypode* sp (3 nests). Within the nests, there were dead hatchlings representing 2.4% of the eggs laid. A further 0.9% of the eggs were represented by live hatchlings that may or may not have escaped from the nests, had they not been excavated. This included 9 hatchlings that were tangled in a buried branch over one nest.

EGG AND HATCHLING PREDATION

There was no evidence of known egg predators such as varanid lizards or large mammals (pigs, dogs, cats) on the island.

Nankeen night herons (*Nycticorax caledonicus*) including adults and fledged juveniles were present in the nesting habitat each night and were observed eating hatchling *N. depressus*. These birds were most concentrated in beach sectors 4-5. At night, up to 6 birds were observed around a nest taking hatchlings as they emerged. This

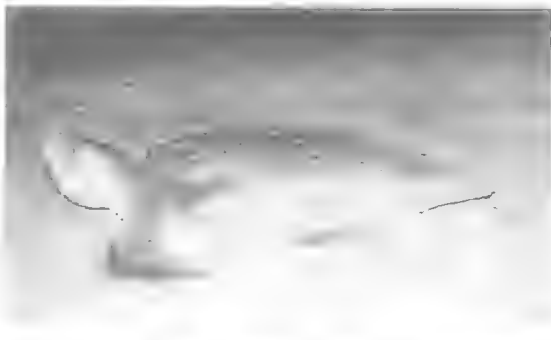


FIG. 7. Adult female *Natator depressus* returning to the sea after nesting on Crab Island.

TABLE 2. Clutch counts and egg measurements recorded from nesting turtles at Crab Island, 6-20 July 1991.* denotes ten eggs measured per clutch.

Species		Mean	SD	range	n
<i>Natator depressus</i>	clutch count	55.9	9.57	34-74	32
	egg diameter(cm)	4.93	0.173	4.52-5.17	60*
<i>Eretmochelys imbricata</i>	clutch count	139.3	10.30	123-151	4
	egg diameter(cm)	3.60	0.071	3.49-3.77	30*
	egg weight (g)	26.08	1.075	24.0-28.0	30*

species was observed also scavenging on turtle eggs that had been dug up by a nesting turtle. Silver gulls (*Larus novaehollandiae*, 1 pair present) flew away with two *N. depressus* hatchlings that had been released from an emerged clutch excavated during the afternoon.

Other potential predators of turtle hatchlings within the nesting habitat and beach area were: water python (*Morelia mackloti*, population estimate not attempted; 1 specimen collected, QMJ31754), estuarine crocodile (*Crocodylus porosus*, minimum of five individuals, including three whose hind foot print lengths were 27, 22.5 and 17.5cm), beach thickknee (*Burhinus neglectus*, several groups of 2-3 birds), osprey (*Pandion haliaetus*, 1 pair), whistling kite (*Haliastur spheurnus*, 1 bird), white breasted sea eagle (*Haliaeetus leucogaster*, 1 pair), frigatebird (*Fregata* sp., 1 bird). Potential predators of turtle hatchlings in the adjacent surf included: Australian pelican (*Pelecanus conspicillatus*, flock of 10), numerous small black-tipped whaler sharks (*Carcharhinus* sp.).

On the team's arrival at the island, there were two recently used fire places with broken *N. depressus* egg shells and fish remains in sectors 5 and 7. During the 17 days the team was at the island, three parties of local residents from adjacent mainland communities visited to collect turtle eggs. Turtle nests were located by probing the sand in old body pits with a spear. All three parties directed their egg collecting activity in sectors 5-8, the area of highest density turtle nesting: 14 July three men collected an estimated equivalent of four clutches of *N. depressus* eggs; 17 July a party of adults and children collected multiple clutches of turtle eggs; 21 July three men collected an undetermined number of turtle eggs. On the 22 July, a fourth party from two dinghies visited the island, but the purpose of their visit was not assessed. One of the nests dug on 14 July contained eggs with dried egg shell, i.e. it was not

freshly laid. The collector expressed the view that these particular eggs were of marginal quality for eating and only half of the clutch was taken and the remainder reburied.

OTHER INCIDENTAL DATA

During a visit on the night of 29 December 1987 to the south of the Jardine River mouth, three *N. depressus* were tagged in the first 100m and several others could be seen further along the beach (E. Evans, in litt.). G. Kyriazis (pers. comm.) walked the beach along the mainland coast from 1 to 3km south of the mouth of the Jardine River during early September 1991. His impression of the track density at this time was that it was comparable to the track density on Crab Island in July 1991. There was one freshly dead *N. depressus* that had died on its return crawl to the sea after nesting. Pigs were recorded to have destroyed most of the hundreds of turtle nests seen on a 6km section of this mainland beach in the early 1980s (B. Gray, pers. comm.) and local residents continue to identify pig, dingo and varanid predation of eggs as common on this beach (G. Kyriazis, pers. comm.). The size range of female turtles tagged while nesting on other occasions during 1987-1991 at Crab Island (n = 19) and the Jardine River mouth (n = 3) are summarised in Table 1. The majority of turtles encountered on these occasions were *N. depressus*.

RECAPTURES

One long distance migration has been recorded from these taggings. An adult female *N. depressus* (T40505), which had been tagged while nesting at Crab Island on 15 January 1990, was captured in a fishing net off Merauke (8°30'S, 140°22'E) in southern Irian Jaya on 10 January



FIG. 8. Adult male *Natator depressus*, tag number B0314, mounted on female prior to capture in approximately 0.7m deep water adjacent to the beach. The female has just surfaced for a breath.

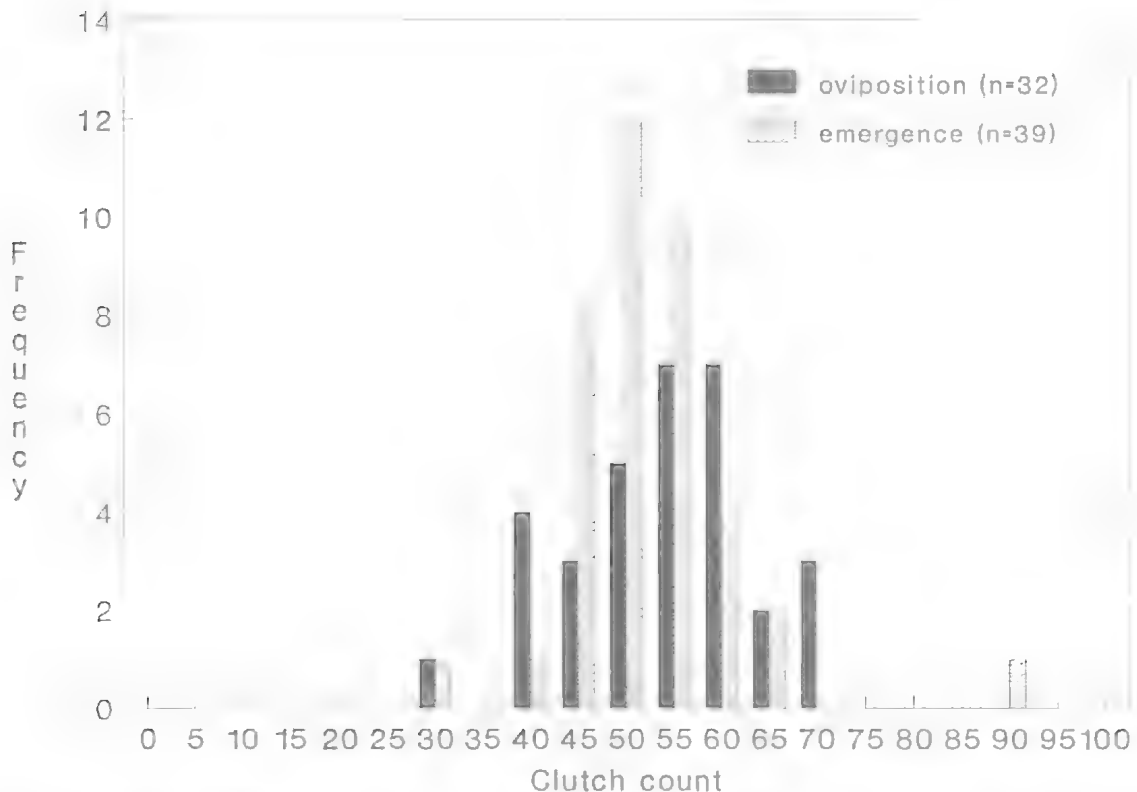


FIG. 9. Frequency distribution of *Natator depressus* clutch counts measured at oviposition and at clutch emergence, Crab Island 6-20 July 1991.

1992. This turtle was eaten. The recapture was made 310km from the nesting beach and two years after she was tagged. This is the first record of *N. depressus* from the coastal waters of Irian Jaya.

One remigration recapture has been recorded from these taggings. *N. depressus* (B1181) was recorded nesting back at Crab Island on 11 September 1992, approximately fourteen months after her initial tagging at Crab Island on 20 July 1991.

DISCUSSION

Marine turtle nesting at Crab Island was first quantified in November-December 1970 (Bustard, 1972). There were subsequent brief visits to further quantify nesting density and to tag nesting turtles during 1976-1979 (Limpus et al., 1983a). As a result of these surveys, Crab Island was found to support all year round breeding and was identified as supporting the largest recorded *N. depressus* nesting population. Low density *E. imbricata* and sporadic *Lepidochelys olivacea*

nesting was also recorded for the island. Specimens of *N. depressus* were collected from Crab Island in January 1981, but the nesting population was not described (Zangerl et al., 1988). The island has remained unsurveyed for marine turtles since August 1979. Limpus et al. (1989) identified that *N. depressus* nesting occurs widely in western Torres Strait, with another large nesting concentration at Deliverance and Kerr Islands. The results of the present study allow for a re-evaluation of the status of this significant turtle rookery after 12 years.

Marine turtles typically lay multiple clutches within a single nesting season at approximately two weekly intervals, except for *Lepidochelys* spp. (Hirth, 1980; Limpus et al., 1984). Not all individuals in a particular population begin or complete nesting at the same time of the year (Limpus, 1985). At rookeries in eastern Australia where *Caretta caretta* and *Chelonia mydas* have a discrete nesting season, 60-70% of the total nesting population for the year can be expected to be recorded during a two week tagging census at

TABLE 2. Incubation and emergence success recorded from 39 freshly emerged *Natator depressus* clutches excavated for counting on Crab Island, 6-22 July 1991.

		Mean	SD	n	range
emerged hatchlings		42.9	12.99	39	17-87
hatchlings in nest:	live	0.5	1.23	39	0-10
	dead	1.3	2.51	39	0-11
eggs	unhatched	5.7	5.98	39	0-22
	undeveloped	4.1	5.10	39	0-30
	predated	0.2	0.59	39	0-3
clutch count		54.6	9.37	39	34-94
nest depth (cm)		58.3	7.21	39	43-71
Hatching success %		81.54	17.29	39	26.5-100.0
Emergence success %		78.56	18.55	39	25.0-100.0

the peak of the nesting season (Limpus, 1985 and unpublished data). Therefore a two week census of the Crab Island nesting population at the peak of the nesting season also is presumed to sample a similar proportion of the total population. However, there is all year round nesting at Crab Island (Limpus et al., 1983a) and the present study may not have sampled at exactly the peak of the nesting season. Each of these factors would reduce the proportion of the total population sampled during the two week census. Therefore, the estimated 1352-1611 clutches laid during the 14 nights, 6-19 July 1991, indicate that in excess of 2200 female *N. depressus* were breeding at Crab Island during the 1991 breeding season. While there are insufficient data to identify any changes in the size of this nesting population since it was last surveyed during 1976-1979 (Limpus et al., 1983a), Crab Island continues to support the largest recorded breeding aggregation for this marine turtle. However, it should be remembered that many *N. depressus* nest on the adjacent mainland and that the species also nests on the islands extending to the north throughout western Torres Strait (Limpus et al., 1989). The total annual breeding population for *N. depressus* in the Crab Island region (northeastern Gulf of Carpentaria and western Torres Strait) remains imprecise, but must number many thousands of females. There is still no evidence that Crab Island is of anything but minor importance for nesting by other marine turtle species.

As of March 1993, there has been only one reported feeding ground recapture, a female *N. depressus* from the south eastern Irian Jaya coast, out of the many turtles tagged while nesting in the Crab Island region (1040 *N. depressus*, 11 *E.*

imbricata, 1 *E. olivacea*; Bustard, 1972; Limpus et al., 1983a; present study). There have been more than 50 recaptures of *N. depressus* reported from the east coast prawn fishery from inside the Great Barrier Reef (GBR) and central Torres Strait, which had been tagged while nesting at the central Queensland rookeries (Limpus et al., 1983b; C. J. Parmenter, pers. comm.). This suggests that the *N. depressus* population nesting at Crab Island does not migrate from the feeding areas along the eastern Queensland coast. No tagged *N. depressus* from Crab Island has been reported from the northern prawn fishery of the Gulf of Carpentaria and southern Arafura Sea even though several thousand *N. depressus* are captured annually as part of the by-catch of the northern prawn fishery (Poiner & Harris, 1993). This lack of *N. depressus* tag recoveries within the northern prawn fishery contrasts with the occurrence of tag recoveries of *C. caretta* from eastern Australian rookeries in the same fishery (Limpus et al., 1992; Limpus & Reimer, 1993). This suggests that the Gulf of Carpentaria is not a significant feeding area for the *N. depressus* that nest at Crab Island. The one long distance tag recovery demonstrates that the feeding distribution of the Crab Island nesting population extends northwards at least to the southern Irian Jaya coast.

Turtle nesting and hatchling emergence have been recorded at Crab Island on all previous visits (April, May, July, August, November and December) with a seasonal variability in density (Limpus et al., 1983a). The limited data from 1991 also show seasonal variability in nesting density. The high density nesting in July (average 133 beachings per night on the whole beach and

44 beachings per night in sector 5; 77-85% nesting success) contrasts with the low number of clutches emerging at the same time (average 4 emerging clutches per night in sector 5). Because the incubation time for marine turtle eggs is approximately two months, in the absence of evidence of extensive clutch destruction or harvest at Crab Island, these data suggest that the July 1991 nesting density was approximately 10 times the magnitude of the nesting density two months earlier in May 1991. The 6-19 July 1991 nesting density appears to be considerably greater than the density recorded in 15-19 July 1978 but included nights with similar nesting density to that recorded on 13-14 August 1979 (Limpus et al., 1983a). This apparent increase in nesting population as indicated by the July nesting densities could have three different explanations: 1, this between-year vari-

ability could be the result of natural annual fluctuations in the nesting population as has been recorded for *C. mydas* in eastern Queensland (Limpus & Nicholls, 1988); 2, the timing of the peak of the nesting season may vary between months in different years; 3, there may have been an increase in the size of the nesting population. Because of the high fidelity that *N. depressus* displays to particular small nesting beaches (Limpus et al., 1984) the possibility that the apparent increase in the Crab Island nesting population could have resulted from inter-rookery movements is dismissed. More extensive surveys of the rookery are needed before the stability of this population can be reliably assessed. Given the extended breeding season and the wide nesting distribution in western Torres Strait, Crab Island and northwestern Cape York Peninsula, the size and distribution of the breeding population cannot be adequately surveyed by brief visits to single localities as has been the pattern to date.

The data collected on this survey of *N. depressus* from Crab Island (Tables 1,2) provide additional support for the conclusion that the *N. depressus* nesting population from the Crab Island region consists of smaller nesting females laying comparable sized clutches of smaller eggs than those of the nesting population at the southern GBR rookeries (Limpus et al., 1989). The hatchling productivity from undisturbed clutches at Crab Island remains comparable to that recorded in previous studies (Limpus et al., 1983a).

The mid-year high density *N. depressus* nesting and associated incubation of eggs at Crab Island spans the months of lowest rainfall and daily air temperature (Fig. 2). This dry season nesting also

coincides with the predominantly south easterly winds. Therefore the majority of the turtle nesting occurs on beaches with a westerly aspect; these are usually leeward to the prevailing winds and are therefore less likely to be eroded by wind driven surf when most eggs are incubating. Also, by nesting in the dry season, the turtles might be avoiding egg loss through flooding that could result from a raised water table below the dunes during the wet season.

The sand temperature (mean \pm SD) at 50cm depth in the nesting habitat for 6-21 July 1991 of $27.6\pm0.49^{\circ}\text{C}$ was the lowest recorded in any month at Crab Island (12 Dec. 1976 = $29.6\pm1.32^{\circ}\text{C}$, 8-10 Dec. 1978 = $31.4\pm0.88^{\circ}\text{C}$, 27 April-7 May 1978 = $29.4\pm1.21^{\circ}\text{C}$, Limpus et al., 1983a) or at Deliverance Island (2-4 October 1987 = $29.4\pm0.95^{\circ}\text{C}$, Limpus et al., 1989). However, the year round sand temperatures at nest depth in the Crab Island area remain above 24°C , the approximate lower limit for successful incubation of marine turtle eggs from all species (Miller, 1985). This facilitates the observed all year round successful nesting by marine turtles in the Crab Island region, although the mid-summer sand temperatures approach 34°C which is the approximate upper lethal incubation temperature for marine turtle eggs (Miller, 1985). In contrast, at the rookeries in central and southern Queensland, the winter sand temperatures at nest depth fall below 24°C and consequently, successful marine turtle nesting can only occur there during the warmer summer months (Limpus, 1971; Limpus et al. 1981). In northern Australia there has probably been a selective advantage for marine turtles to aggregate their nesting into the mid-year when sand temperatures are well separated from the lethal limits of incubation temperature (Guinea 1993).

The pivotal temperature, the theoretical temperature at which a 1:1 sex ratio could be expected, is not fixed for *Caretta caretta* or *Chelonia mydas* but varies between breeding units. While within each breeding unit, the species reproduces regionally on beaches that provide a range of nest temperatures spanning the pivotal temperature (Limpus et al., 1983c; C. Limpus, unpublished data). The pivotal temperature for *N. depressus* from the southern GBR region is 29.5°C , ranging from 100% male hatchling production at 28°C to 100% females at 31°C (C. Limpus, unpublished data). Based on the recorded sand temperatures at Crab Island (see above), if the Crab Island region population had

the same pivotal temperature as the southern GBR population, Crab Island would be producing mostly male hatchlings during the mid-year high density nesting, while mostly females would be produced from the low density summer nesting. However, if the Crab Island region nesting population is part of a separate breeding unit from the southern GBR population, then different pivotal temperatures could occur for the populations. This would then allow for the possibility of the Crab Island nesting population fitting the model that a turtle breeding unit chooses its nesting beaches such that its pivotal temperature occurs within the range of sand temperatures at nest depth that is available during the main nesting season. This would require that the Crab Island region and southern GBR nesting populations represent different *N. depressus* breeding units. The differences in adult and egg size between the northeastern Gulf of Carpentaria and southern GBR *N. depressus* populations also support the hypothesis that these populations are separate stocks. A precise estimate of the *N. depressus* hatchling sex ratio from Crab Island cannot be made from the available data.

The local peoples of northern Cape York Peninsula, western Torres Strait and Irian Jaya harvest small numbers of adult *N. depressus* and numerous clutches of eggs annually from this population (Johannes & MacFarlane, 1991; Limpus et al., 1983a, 1989; present study). The impact of each of these village-based harvests should not be considered in isolation. Indeed, the harvest at any one nesting beach or by any one village should be assessed within the regional context of the total breeding population. In relation to this, the significance of egg losses through harvest and predation to the regional population poses major uncertainties. If the mainland beaches have a different sand composition and hence sand colour, they would have a different temperature profile from the islands. In particular, darker sands would be warmer and result in a higher proportion of females from these mainland beaches (c.f. the situation for *Caretta caretta* in southeastern Queensland, Limpus et al., 1983c). The indicated high predation levels by pigs, dingoes and varanid lizards on the eggs laid on the mainland beaches has the potential for threatening the survival of the entire population in the long term. The observed egg harvest by local people of a few clutches each week from Crab Island could be sustainable during the mid-year high density nesting. However, if the rate of harvest is constant throughout the year and the off-

peak nesting produces mostly female hatchlings, then the loss of additional female hatchling production through egg harvest must be considered in conjunction with the impact of the egg predation on mainland clutches. In addition, what impact the drowning hundreds of *N. depressus* annually in fishing gear in the northern prawn fishery (Poiner & Harris, 1993) and other Gulf of Carpentaria fisheries (P. Couper, unpublished data) has on the Crab Island nesting population needs clarification. These *N. depressus* mortalities in the dispersed feeding areas represent additional losses to this population that have commenced in recent decades. Before it can be judged as to whether the current level of harvest of *N. depressus* eggs and turtles by the local peoples from these rookeries of the northeastern Gulf of Carpentaria and western Torres Strait is sustainable, the breeding unit of these turtles needs to be aligned to geographic boundaries and population size and anthropomorphic mortality for the population throughout its range quantified. In addition hatchling productivity and associated sex ratio should be quantified from the significant rookeries within the region. When these types of data are available, the long term viability of this most significant *N. depressus* population and the associated harvests can be more reliably assessed.

ACKNOWLEDGEMENTS

This research was conducted as a collaborative project between the Queensland Turtle Research Project of the Queensland Department of Environment and Heritage and the Queensland Museum. Permission to conduct the research on Crab Island was granted by the Injinoo Community Council. The Thursday Island meteorological data were supplied by the Australian Bureau of Meteorology. George, Sandyl, Nicky and Zoe Kyriazis, Nola Collins and Elizabeth Evans assisted in tagging and field data collection. George Kyriazis, in addition, provided the transport for the team between Bamaga and Crab Island and assisted in establishing the camp. Jeff Wright printed the photographs. Bronwyn Perkins prepared the map. This assistance is gratefully acknowledged.

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PANDARID COPEPODS PARASITIC ON SHARKS FROM NORTH QUEENSLAND WATERS. *Memoirs of the Queensland Museum* 33(1): 290-1993. The Pandaridae are ectoparasitic caligoid copepods exclusive to elasmobranchs. 38 species are known worldwide (Cressey, 1967, 1970; Rangnekar & Rangnekar, 1972; Cressey & Boyle, 1978; Cressey & Simpfendorfer, 1988).

In a checklist of fish parasites from Australian waters, Beumer et al. (1983) listed 8 pandarid species based on records in two published studies of Australian copepod parasites (Heegaard, 1962; Kabata, 1966). Beumer et al. (1983) followed Cressey (1967) in synonymising *Dinemoura* Burmeister, 1833 with *Dinemoura* Latreille, 1829. However, they did not follow Cressey by regarding *Nesippus australis* Heegaard, 1962 and *N. incisus* Heegaard, 1962 as separate from *N. orientalis* Heller, 1868, or by regarding *Perissopus serratus* Heegaard, 1962 as separate from *P. dentatus* Steenstrup & Lütken, 1861. Beumer et al. (1983) thus contained 6 valid species: *Dinemoura latifolia* (Steenstrup & Lütken, 1861), *D. producta* (Müller, 1785), *Echthrogaleus coleopranus* (Güérin-Mèneville, 1837), *Nesippus orientalis* Heller, 1868, *Pandarus bicolor* Leach, 1816, and *Perissopus dentatus* Steenstrup & Lütken, 1861. Cressey & Simpfendorfer (1988) added *Pseudopandarus australis* to the species known from Australian waters. This note reports the occurrence of 3 pandarid species on sharks from Cleveland Bay (19°15'S, 146°50'E), north Queensland, and provides information on their hosts. Sharks were caught between Feb. 1986 and Jan. 1988 using gillnets, longlines, otter trawls and handlines. The parasites were identified using keys in Yamaguti (1963) and Cressey (1967).

Three species were identified: *Pandarus niger* Kirtesinghe, 1950 (QMW12207, 12212); *Perissopus dentatus* Steenstrup & Lütken, 1861 (QMW12208, 12209, 12456, 12462, 12464); and *Pseudopandarus australis* Cressey & Simpfendorfer, 1988 (QMW12210, 12211). The occurrence of *P. niger* is a

Sharks	Specimens examined	<i>Pandarus niger</i>	<i>Perissopus dentatus</i>	<i>Pseudopandarus australis</i>
<i>Carcharhinus leucas</i>	16	-	100	12.5
<i>C. fitzingerensis</i>	30	-	50	
<i>C. macroti</i>	1	-		
<i>C. noronhai</i>	28	21.4	21.4	
<i>C. tilstoni</i>	45	-	91.4(2.2)	
<i>Rhizoprionodon acutus</i>	47	-		61.7(2.1)
<i>R. taylori</i>	201	-	1.0	36.8(3.0)
<i>Hemigaleus microstoma</i>	4	-	75	25(25)
<i>Sphyrna lewini</i>	91	1.1	10.6	1.1
<i>S. mokarran</i>	1	-	100	-

Table 1. Rates of occurrence of pandarid copepods on sharks of Carcharhinidae(C), Hemigaleidae(H), and Sphyrnidae(S). Rates given are for females; where present, rate for males given in brackets.

new record for Australian waters. It has previously been reported from Sri Lanka (Kirtesinghe, 1950) and Taiwan (Cressey, 1967) on sharks from the family Carcharhinidae. It is widespread in tropical Australian waters, regularly occurring on *C. noronhai* in the Northern Territory (J. Lyle, pers. comm.; QMW12460, 12461).

P. dentatus is abundant and widespread in tropical and subtropical oceans, and previous workers have reported it from 29 species of shark (Yamaguti, 1963; Cressey, 1967, 1970; Hewitt, 1967; Russo, 1975; Beumer et al., 1983). Only one of the 8 host species of *P. dentatus* recorded for Cleveland Bay (*Sphyrna lewini*) has previously been reported (Hewitt, 1967).

Rates of occurrence were variable between both host and pandarid species, with female pandarids occurring more frequently, and on more host species, than males (Table 1). The three families of sharks on which the pandarids were recorded are all active, free swimming and closely related (Compagno, 1988). Two benthic shark species (*Chiloscyllium punctatum* and *Stegastoma fasciatum*) — from a different order — had no pandarids on them.

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A HUMPBACK WHALE CALF AND TWO SUBADULT DENSE-BEAKED WHALES RECENTLY STRANDED IN SOUTHERN QUEENSLAND

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Paterson, R.A., Quayle, C.J. & Van Dyck, S.M. 1993 06 30: A Humpback Whale calf and two subadult Dense-beaked Whales recently stranded in southern Queensland. *Memoirs of the Queensland Museum* 33(1): 291-297. Brisbane. ISSN 0079-8835.

A new born Humpback Whale calf (*Megaptera novaeangliae*) and two subadult Dense-beaked Whales (*Mesoplodon densirostris*) recently stranded on the southern Queensland coast. The *M. densirostris* skeletons were recovered together with various soft tissue material. The post-cranial skeleton of the *M. novaeangliae* was not recovered. The larynges of the three specimens were examined in detail. □ *Humpback Whale, Dense-beaked Whale, stranding, Queensland.*

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Opportunities to examine stranded balaenopterid and ziphiid whales, with the exception of Minke Whales (*Balaenoptera acutorostrata*), on the Queensland coast are limited (Paterson & Van Dyck, 1990, 1991). Recently, material recovered from a new born Humpback Whale *Megaptera novaeangliae* and two subadult Dense-beaked Whales *Mesoplodon densirostris* was a valuable addition to the cetacean collection in the Queensland Museum. The *M. novaeangliae* specimen is registered JM8658 and the *M. densirostris* specimens are registered JM8807 and JM9640.

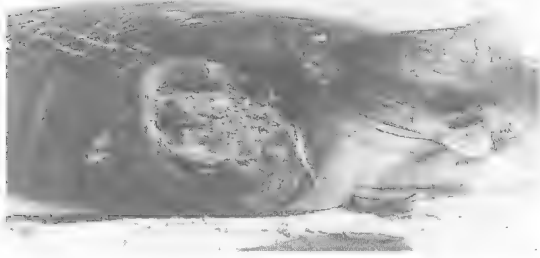


FIG. 1. Shark bites on left side of *Megaptera novaeangliae* JM8658. The anterior bite extended deeply into the thoracic muscles.

SPECIMEN DESCRIPTIONS

HUMPBACK WHALE

JM8658 was a 4.7m long new born (umbilicus unhealed) female that stranded alive during the afternoon of 19 July, 1991 at Eager's Creek (27°07'S, 153°27'E) on the oceanic shore of Moreton Island. Two large non-bleeding shark bites were noted on the left side of the body as



FIG. 2. Extensive superficial rakes on *Megaptera novaeangliae* JM8658. They are considered to be caused by sharks.

well as numerous superficial rakes (Figs 1,2). The whale was refloated and pushed into the surf but was found dead at the same location a few hours later. We examined the carcass three days later. The larger of the previously noted bites extended deeply into the thoracic muscles and its edges showed signs of early healing indicating that the shark attack was not an immediate pre-stranding event.

Material collected included the skull and mandible, blubber and skin samples (the latter for



FIG. 3. Recent and healed 'cookie-cutter' lesions on *Mesoplodon densirostris* JM8807.



FIG. 4. Close-up view of 'cookie-cutter' lesions on *Mesoplodon densirostris* JM8807. The throat groove characteristic of ziphiids is also demonstrated.

DNA study) and the larynx. The mid-dorsal blubber thickness was 2.8cm and is consistent with recent birth. Comparative blubber thicknesses from a *M. novaeangliae* calf, approximately four weeks old, and a yearling in the Queensland Museum collection are 4.5cm and 9.7cm respectively. The right baleen row numbered 340 ± 5 , consistent with the range for the species (Matthews, 1937). The largest baleen plates measured 8.5cm in length.

The stranding of a new born *M. novaeangliae* at latitude 27°S in July confirms previous sighting reports (Chittleborough, 1965; Paterson & Paterson, 1984, 1989) that occasional calving occurs during the northern migration of the species along the Australian coast at latitudes higher than those



FIG. 5. Left, *Mesoplodon densirostris* JM8807. Radiograph of left pectoral flipper demonstrating distal aspects of radius and ulna, carpus, metacarpals and phalanges. Skeletal immaturity is evident. The ossification centre for the peripheral unciform has not yet appeared. Right, *Mesoplodon densirostris* JM9640. Radiograph of left pectoral flipper showing eight carpal bones compared with seven in JM8807. (The triangular structure overlying the distal ulna is frozen soft tissue from the axillary region.)

at which calving is generally considered to occur (Chittleborough, 1953; Simmons & Marsh, 1986; Townsend, 1935).

DENSE-BEAKED WHALES

JM8807 was a 3.8m long female found dead at dawn on 22 October, 1991 at Main Beach, Point Lookout (27°26'S, 153°33'E) on North Stradbroke Island. Recent and healed superficial 'cookie-cutter' lesions were noted and they coalesced ventrally (Figs 3,4). They were similar to, but not as extensive as, those noted in a mature

male *M. densirostris* described by Paterson & Van Dyck (1990). The whale was dark grey dorsally and lighter grey ventrolaterally, particularly in the umbilical and genital regions and around the V-shaped throat groove characteristic of ziphiids.

We examined the carcass the day after its discovery. The entire skeleton was collected. The vertebral formula C7; T9; L10; Cdl8=44 is less than counts of 46 and 47 in two *M. densirostris* from the Atlantic coast of North America and 45 in a specimen from Lord Howe Island (Raven,

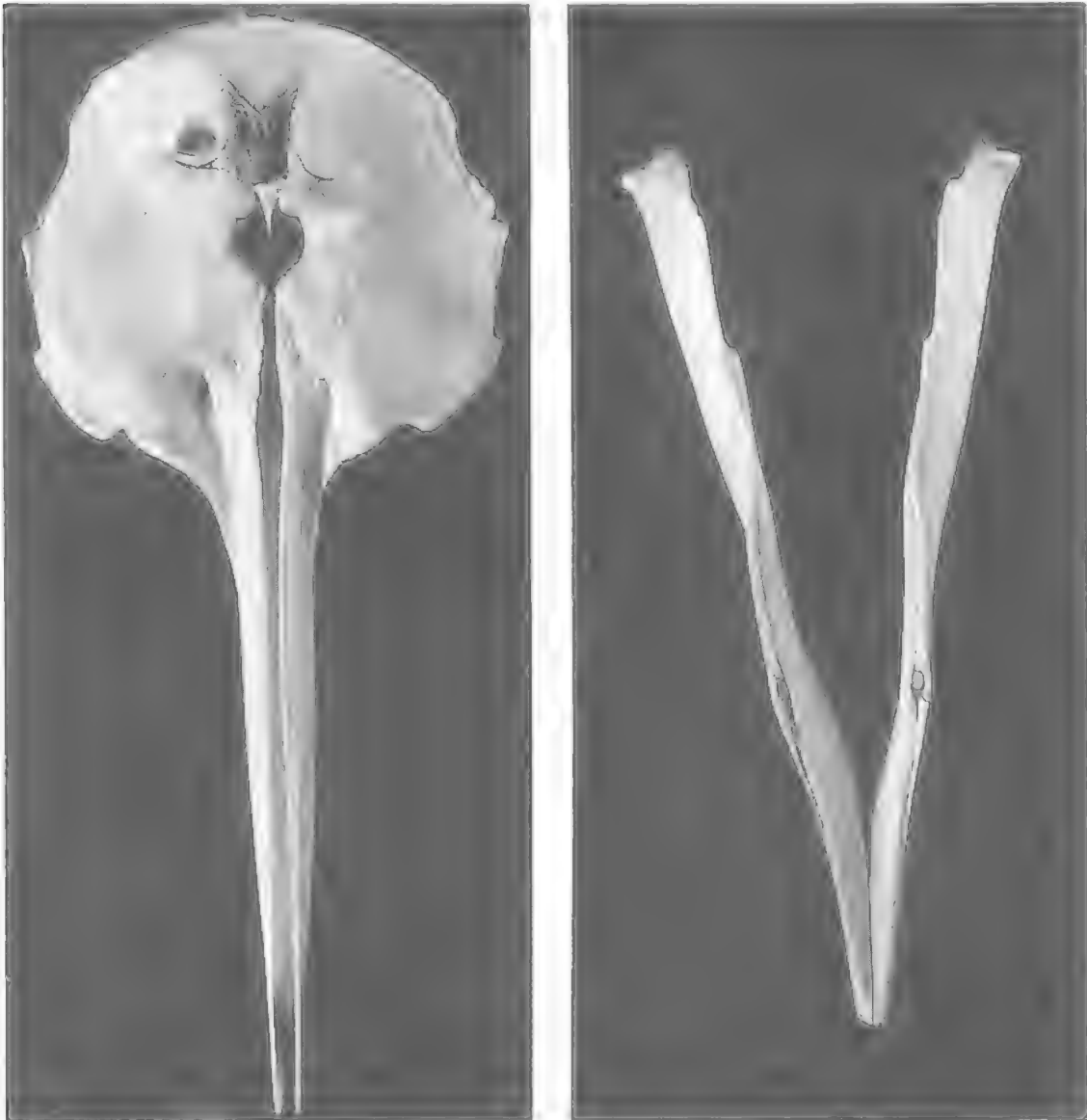


FIG. 6. *Mesoplodon densirostris* JM8807: left, dorsal aspect of skull; right, dorsal aspect of mandible.



FIG. 7. *Mesoplodon densirostris* JM8807. Left lateral mandibular radiograph demonstrating unerupted tooth characteristic of females.

1942) but is within the range described by Ross (1984). The size discrepancy between the penultimate and last caudals suggests the possibility that one caudal was lost during preparation. With the exception of the coalesced proximal three cervical vertebrae, the central epiphyses of all vertebrae were unfused. The phalangeal formula, derived from a radiograph of the left pectoral flipper (Fig. 5), is I:1, II:4, III:4, IV:3, V:2, which differs slightly from that reported by Kasuya & Nishiwaki (1971) in a Formosan specimen of *M. densirostris*. They (p.133 & fig.1) appear to have included the metacarpals in the formula. The skull and mandible are shown in Fig. 6. The characteristically shaped unerupted mandibular tooth of female *M. densirostris* is demonstrated radiographically in Fig. 7. The tooth measured 52mm in height, 30mm in length and 9mm in greatest diameter. Its pulp cavity was completely unfilled.

Moderate nematode (*Anisakis* sp.) and acanthocephalan (*Bolbosoma vasculosum*) infestation was noted in the stomach and intestine respectively. The gastro-intestinal tract was otherwise empty.

One ovary was collected. Its external features

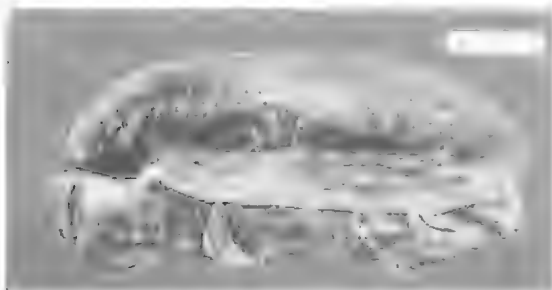


FIG. 8. *Mesoplodon densirostris* JM8807. External ovarian features. Scale in mm.

are shown in Fig. 8. Histological examination was reported as follows:

The ovary contains numerous primordial follicles, a few secondary follicles, occasional cystic atretic follicles and some small hyaline scars which may represent corpora albicans. No corpora lutea can be identified.

The presence of secondary follicles indicates sexual maturity is, at least, approached. It is uncertain whether ovulation has occurred. If the small scars are true corpora albicans this would indicate that ovulation had taken place but the evidence is insufficient to establish this with certainty.

Although the ovarian histological evidence indicates that this 3.8m long animal was approaching sexual maturity, the lack of epiphyseal fusion indicates physical immaturity. The dental, sexual and physical development of JM8807 was similar to that of the 3.56m long Formosan specimen described by Kasuya & Nishiwaki (1971).

JM9640 was a 3.65m long female found dead during the morning of 21 June, 1992 at Cathedral



FIG. 9. 'Cookie-cutter' lesions and characteristic throat groove of ziphiids on *Mesoplodon densirostris* JM9640.

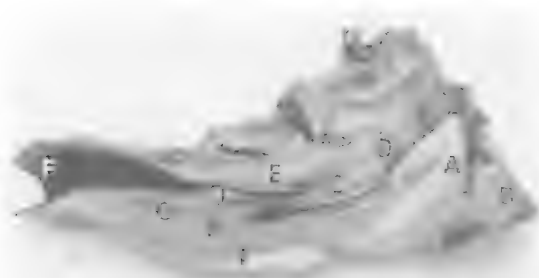


FIG. 10. Larynx *Megaptera novaeangliae* JM8658 in longitudinal section, medial aspect, with thyroid cartilage removed: (A) epiglottic cartilage; (B) fibrous attachment to thyroid cartilage; (C) arytenoid cartilage-corpus; (D) arytenoid cartilage-rostral end; (E) cricoid cartilage; (F) tracheal lumen; (G) fundus of ventral diverticulum; (H) neck of the ventral diverticulum; (I) thyroarytenoid muscle; (J) interarytenoid fibro elastic connection.

Beach (25°10'S, 153°13'E) on Fraser Island. 'Cookie-cutter' lesions of similar distribution to those on JM8807 were evident as well as the characteristic throat groove (Fig. 9).

We were unable to visit the stranding site to examine the whale but arranged for its head and a pectoral flipper to be removed and frozen so that they could be subsequently studied in a fresh state. The remainder of the carcass was buried in sand dunes behind the beach and the skeleton was retrieved two months later. The vertebral epiphyseal status and vertebral formula (C7; T9; L10: Cdl8 = 44) were identical to JM8807 but the last caudal may have been lost. Unfortunately numerous rib and vertebral fractures had occurred during transportation of the carcass to the sand dunes and those fractures detract from the specimen's quality.

The phalangeal formula I:1, II:4, III:4, IV:3, V:2 is identical to JM8807. The carpus contains

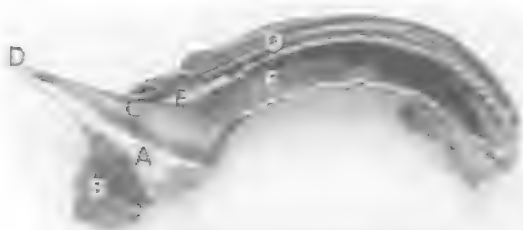


FIG. 11. Larynx *Mesoplodon densirostris* JM8807 in longitudinal section, medial aspect, with thyroid cartilage removed. (A) epiglottic cartilage; (B) fibrous attachment to thyroid cartilage; (C) arytenoid cartilage-corpus; (D) arytenoid cartilage-rostral end; (E) cricoid cartilage; (F) tracheal lumen; (O) oesophagus.

eight bones (Fig. 5) compared with seven in JM8807 and the Formosan specimen. Raven (1942) demonstrated eight carpal bones in an adult male *M. densirostris*. We presume that the ossification centre of the peripheral unciform had not yet developed in either JM8807 or the Formosan specimen but are surprised at the apparent late development of this bone which is larger than its neighbours in both JM9640 and the specimen illustrated by Raven (1942).

The left tooth measured 54mm in height, 47mm in length and 10mm in greatest diameter. Its pulp cavity was extensively obliterated. On the basis of the dental and carpal development we conclude that JM9640 was more mature than JM8807.

LARYNGEAL STRUCTURE

Various authors, including Benham (1901) and Hosokawa (1950), have compared the larynges of mysticetes and odontocetes. The former are characterised by a large ventral diverticulum surrounded by the thyro-arytenoid muscle and the latter by the aryteno-epiglottideal tube, an upward extension of the fused arytenoid and epiglottic cartilages into the choana. Those features have been demonstrated in JM8658, JM8807 and JM9640.



FIG. 12. Larynx and oesophagus *Mesoplodon densirostris* JM8807 from dorsal aspect. The bossed tip of the aryteno-epiglottideal tube is shown on the right. (C) arytenoid cartilage-corpus; (D) arytenoid cartilage-rostral end; (F) trachea; (O) oesophagus.

The larynx of JM8658 is shown in longitudinal section in Fig. 10 and the salient anatomical structures have been annotated in conformity with the description by Quayle (1991) of the larynx of a male *M. novaeangliae* of similar development to JM8658. There is no appreciable difference between those male and female specimens.

Quayle (1991) considered that phonation could occur between the apposing arytenoids in mysticetes although true vocal cords were not evident. He also proposed a functional role for the ventral diverticulum in the production of the complex sounds of *M. novaeangliae*. Mysticetes presumably generate high pressures within the oral cav-

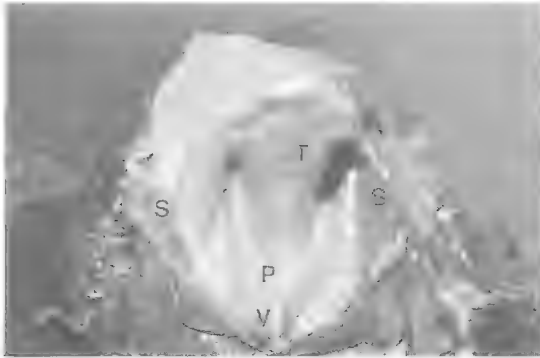


FIG. 13. Laryngo-pharynx *Mesoplodon densirostris* JM9640 from rostral aspect. (P) palato-pharyngeus; (S) superior constrictor of pharynx; (T) aryteno-epiglottideal tube; (V) vomerine attachment of palato-pharyngeus.

ity and pharynx during feeding when large volumes of water are forced through the baleen. The ventral diverticulum may have an additional function in assisting to prevent water from entering the trachea.

The larynx of JM8807 is shown in longitudinal section (Fig. 11) as well as from its dorsal aspect (Fig. 12). The aryteno-epiglottideal tube is bossed at its tip and was closely applied to the posterior narial canal. The almost complete fusion of the arytenoid and epiglottic cartilages and their relationship to the posterior nares more effectively separates the aero-digestive tracts in this odontocete compared with JM8658.

The fresh laryngo-pharynx of JM9640 is shown in Figs 13,14,15. In Fig. 13 the aryteno-epiglottideal tube is demonstrated from the rostral aspect and a large muscular cuff (the superior constrictor of the pharynx) is noted peripherally. The margin of this muscle has been dissected from the bony posterior choana. A circular muscle, whose mar-



FIG. 14. Laryngo-pharynx *Mesoplodon densirostris* JM9640 from lateral aspect. (F) trachea; (O) oesophagus; (P) palato-pharyngeus; (S) superior constrictor; (T) aryteno-epiglottideal tube; (W) oro-pharynx.

gin was partially separated from the superior constrictor appeared to 'grip' the aryteno-epiglottideal tube. This circular muscle is the palato-pharyngeus (Hosokawa, 1950) and it had an anterior attachment to the vomer. The disposition of the superior constrictor and the palato-pharyngeus to the aryteno-epiglottideal tube in the lateral position is demonstrated in Fig. 14. We postulate that the superior constrictor in combination with the palato-pharyngeus may act inter alia to expel water from the choanal region. In Fig. 15 the laryngo-pharynx is shown in wider perspective and the palato-pharyngeus has been partially retracted. A large probe has been passed through the oro-pharynx. It traverses the pyriform fossa (which is beside the larynx) and enters the oesophagus. This further demonstrates the separation of the aero-digestive tracts in this odontocete.

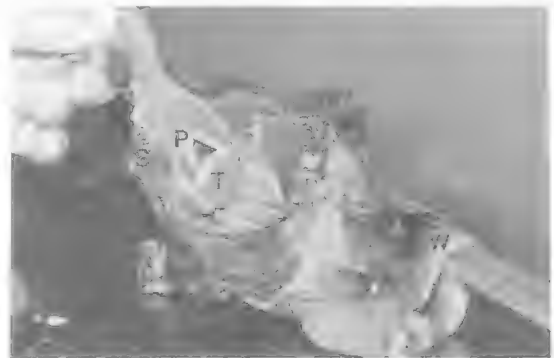


FIG. 15. Laryngo-pharynx *Mesoplodon densirostris* JM9640 from dorso-rostral aspect. The large probe is seen in the oro-pharynx. It was passed through the left pyriform fossa to enter the oesophagus which is obscured by the retracted superior constrictor and palato-pharyngeus. (P) palato-pharyngeus; (S) superior constrictor; (T) aryteno-epiglottideal tube; (W) oro-pharynx.

In this fresh specimen it was not possible to retract the aryteno-epiglottideal tube. Pilleri (1979) considered, on the basis of acoustic experiments, that the aryteno-epiglottideal tube was retracted during deglutition and disagreed with Rawitz (1900) who stated that food passed to the side of the larynx. Our opinion, based on morphological considerations, concurs with that of Rawitz.

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Committee photographed JM8658 and Reg Lambert photographed JM8807. Brendan McLarty of QNPWS secured JM8658 and transported us to the stranding site. Lis Sedlak-Weinstein of the University of Queensland examined JM8807 for parasites and assisted with retrieval of the specimen. John Ford of QNPWS photographed JM9640 and secured the specimen. Paul Stumkat of the Queensland Museum retrieved its skeleton. John Musgrave of Sullivan, Nicolaidis and Partners arranged the histological examination of JM8807 and Stephen Marmo of the X-ray Department, Royal Brisbane Hospital took the radiographs. Bruce and Carolyn Cowell patiently and skilfully photographed and prepared material at the Queensland Museum and Jeff Wright took some of the laryngeal photographs.

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BRACONINE WASPS OF AUSTRALIA

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An illustrated key to the 45 genera of Braconinae known from Australia is provided. *Pycnobraconoides* gen.nov. (type species: *Ichneumon mutator* Fabricius) is described and illustrated. Thirteen new species are described and illustrated: *Acrocerilia tricolor* sp.nov. (Queensland); *Africadesha tobiasi* sp.nov. (Queensland); *Atanycolus australiensis* sp.nov. (Queensland); *Calcaribracon willani* sp.nov. (Queensland); *Furcadesha walteri* sp.nov. (Queensland); *Myosoma rufescens* sp.nov. (Queensland); *Pedinopleura australiensis* sp.nov. (Queensland); *Simplicibracon nigratarsus* sp.nov. (Queensland); *Testudobracon australicolorus* sp.nov. (Queensland); *Testudobracon tatyanae* sp.nov. (Queensland); *Testudobracon unicolorus* sp.nov. (Queensland); *Trigastrotheca tricolor* sp.nov. (Queensland) and *Virgulibracon endoxylaphagus* sp.nov. (Queensland). *Poecilobracon* Cameron is treated as junior synonym of *Callibracon* Ashmead. *Bracon froggatti* Cameron is transferred to *Pycnobraconoides* gen.nov. Nine genera are recorded from Australia for the first time: *Acrocerilia* van Achterberg; *Africadesha* Quicke, *Atanycolus* Foerster, *Furcadesha* Quicke, *Gelasinibracon* Quicke, *Paranesaulax* Quicke, *Rostraulax* Quicke, *Trigastrotheca* Cameron and *Vipiomorpha* Tobias. *Calcaribracon diores* (Cameron) is recorded from Australia for the first time. Notes are provided on the distributions and biologies (when known) of all the genera. □ Hymenoptera, Braconidae, Braconinae, wasp, parasite, Australia, key, new genera, new species, synonymy.

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The Braconinae is a huge, cosmopolitan subfamily of parasitic wasps with nearly 5000 described species (Shenefelt, 1978) distributed among more than 200 genera worldwide. The vast majority of species are ectoparasitoids principally on coleopterous and lepidopterous hosts though a few attack Diptera, Hymenoptera-Symphyta and possibly Homoptera and one group, the Aspidobraconina, are endoparasitic on butterfly pupae.

Only a minority of extant species have been described and there are also undoubtedly numerous new genera awaiting discovery, the Australian fauna of braconine wasps being particularly poorly known. The last generic key dealing specifically with Australia is that of Szépligeti (1906) which included 10 genera. More recently, Parrott (1953) catalogued the Australian Braconinae listing 12 genera compared with the 45 now known to occur there. More Australian species can be identified to genus with the key to the Old World genera provided by Quicke (1987b). However, since that time, several new Australian genera have been described (Quicke, 1988c, 1989d; Quicke & Tobias, 1990) and it is therefore thought that the presentation of an illustrated key to the Australian genera would be both timely and

would encourage much needed investigation of Australian braconine wasp biology.

TERMINOLOGY AND COLLECTIONS

Terminology follows that of van Achterberg (1979, 1988). Wing veins are measured from the centres of their junctions (except for forewing vein r and where otherwise stated), length of head is measured perpendicular to the face (re: couplet 34), length of femur excludes trochantellus and ovipositor length refers to that part which would normally project beyond the apex of the metasoma when directed posteriorly as in most set specimens.

Abbreviations for museums are: American Entomological Institute, Gainesville (AEIG); Australian Museum, Sydney (AMSA); Australian National Insect Collection, Canberra (ANIC); Hungarian Natural History Museum, Budapest (HNHM); Natural History Museum, London (BMNH); Queensland Department of Primary Industries, Indooroopilly, Brisbane (QDPI); Queensland Museum, South Brisbane (QMBA); Quicke Collection, Sheffield (QC).

KEY TO THE GENERA AND SUBGENERA OF AUSTRALIAN BRACONINAE (♀ ♀ ONLY)

The following key is arranged so as to obtain reasonably quick identification of Australian genera and thus the first key character is chosen so as to divide the known genera into two, roughly equal-sized groups. By reference to Figures 27-35 the shape of the scapus of the great majority of specimens encountered should be unambiguously assignable to one category or the other. The few genera with species showing variation or intermediate conditions (notably in the *Aphrastobraconina*, viz. *Cedilla*, *Curriea*, *Ligulibracon*, *Megalommum* and *Undabracon* and especially *Eucurriea*) are allowed for by a loop. To assist further with use of couplet 1, and to help allow for specimens in which both antennae are missing, a list of unique characters for genera and groups is provided in Table 1.

1. Scapus shorter ventrally than dorsally in lateral aspect when directed anteriorly, usually small (Figs 27, 28, 31, 47, 48, 75, 76, 81, 85), not emarginate medially (Fig. 47) and at most only weakly emarginate laterally (Figs 31, 47) (see Table 1 in case of uncertainty) 2
 - Scapus at least as long or longer ventrally than dorsally in lateral aspect when directed anteriorly, often cylindrical and large (Figs 32-35, 39, 44, 80), usually with well-developed apico-medial and apico-lateral emarginations 32
2. Forewing vein CU1a arising at the same level as 2-CU, vein CU1b much longer than 3CU-1 if the latter is distinct (Fig. 12) (*Adeshim*) 3
 - Forewing vein CU1a arising well below the level of 2-CU, vein 3CU-1 at least as long as and usually much longer than vein CU1b (Figs 13, 15, 19, 94, 100) 4
3. Posterior margin of 5th metasomal tergite strongly produced on either side of the midline (Figs 110, 111) *Furcadesha*
 - Posterior margin of 5th metasomal tergite not produced sub-medially *Africadesha*
4. First metasomal tergite fused to metasomal syntergite 2+3, the junction between tergites 1 and 2 being represented by a crenulate sulcus (Figs 74, 121) (*Aspidobraconina*) 5
 - First metasomal tergite movable joined to metasomal syntergite 2+3, there being a normal arthrodial intersegmental membrane between tergites 1 and 2 (Figs 59-71) 6
5. Median area of metanotum with a complete mid-longitudinal carina; dorsal carinae of 1st metasomal

- tergite running separately to posterior margin of tergite; base of hindwing with a glabrous area; median lobe of mesoscutum with a pair of sub-medial, longitudinal grooves anteriorly; 6th tergite with relatively shallow peri-basal, transverse groove (Fig. 121) *Pedinopleura*
- Median area of metanotum without a complete carina (Fig. 105); dorsal carinae of 1st metasomal tergite uniting mid-posteriorly well before posterior margin of tergite (Fig. 74); base of hindwing more or less evenly setose; median lobe of mesoscutum without sub-medial longitudinal grooves anteriorly; 6th tergite with deep peri-basal, transverse groove (Fig. 115) *Hyboteles*
- 6. Propodeum with a complete, lamelliform mid-longitudinal carina (see Fig. 105) 7
 - Propodeum without a complete lamelliform mid-longitudinal carina or with only a short one posteriorly 12
- 7. Posterior margin of 6th metasomal tergite with a (usually) deep, narrow, semicircular, medial emargination (Figs 117, 118, 120) and (usually) tergites 3-5 distinctly roundly produced laterally (Figs 116, 119); metasomal syntergite 2+3 wider than long; ovipositor as long as or longer than the metasoma *Tesudobracon*
 - Posterior margin of 6th metasomal tergite not narrowly emarginate medially nor roundly produced laterally (Fig. 113); metasomal syntergite 2+3 longer than wide (Figs 71, 73); ovipositor usually shorter than half the metasoma 8
- 8. Posterior margin of 6th metasomal tergite with a pair of submedian emarginations leaving a sharp median prominence (Figs 112, 113) *Trigastrotheca*

Character	State	Go to key couplet
Scapus	petiolate, strongly or angularly narrowed at base with concave basal profile (Fig 44)	10
Propodeum	with a complete, mid-longitudinal (usually lamelliform) carina (Fig 105)	2
Forewing vein 3-CU1	absent or much shorter than vein CU1b (Figs 12, 89)	1
Forewing veins CU1b	much wider than posterior part of vein 3CU1 (Figs 21, 22, 94)	12
Claws	bifurcate (Figs 57, 58)	42
Basal lobe of claw	pointed or with small accessory tooth (Figs 52-54)	3
1st metasomal tergite	fused to syntergite 2 (Fig 74)	5

TABLE 1. Characters characterizing and unique to genera or groups of genera and key couplet to proceed from to complete identification

- Posterior margin of 6th metasomal tergite without submedial emarginations nor with a median prominence 9
- 9. Base of hindwing with a large glabrous area distal to, and approximately the same size as, the sub-basal cell; scutellum with a well-developed pit medio-anteriorly; forewing vein r-m with only a single posterior bulla; forewing 2nd submarginal cell virtually parallel-sided, veins 3-SR and 2-M not noticeably converging distally *Acrocerilia*
- Base of hindwing more or less evenly densely setose with at most only a small glabrous area around vein 2-1A; scutellum without a medio-anterior pit; forewing vein r-m variable but often with a distinct bulla and associated flexion line anteriorly as well as posteriorly; forewing 2nd submarginal cell narrowing distally 10
- 10. Hindwing vein 2-SC+R transverse (Fig. 102); ovipositor (part extending beyond apex of metasoma) longer than the median length of the 2nd metasomal tergite; transverse median clypeal carina strongly protruding (Fig. 76) *Simplicibracon*
- Hindwing vein 2-SC+R longitudinal (Fig. 101); ovipositor (part extending beyond apex of metasoma) shorter than median length of 2nd metasomal tergite; transverse median clypeal carina less strongly protruding 11
- 11. Precoxal suture represented by a deep, smooth, medial, circular pit; 2nd metasomal suture interrupted medially at least by a strong ridge, usually by a wider area (Figs 71, 73); median area of metanotum with a complete mid-longitudinal carina *Gelatinibracon*
- Precoxal suture represented by an elongate distinctly sculptured impression, 2nd metasomal suture not interrupted medially; median area of metanotum bulbous, without a complete mid-longitudinal carina *Esengoides*
- 12. Basal lobes of claws at least angularly narrowing before the claw (Figs 53, 54), sometimes produced into a distinct tooth-like process (Fig. 52) 13
- Basal lobe of claws smoothly curved (Figs 55-57) 20
- 13. Hindwing with at least a pigmented line representing vein 3-CU (Fig. 14; separated from remainder of venation); basal lobe of claws produced into a tooth-like process (Fig. 52) 14
- Hindwing without vein 3-CU (Figs 15-19); basal lobe of claws angularly narrowed, but not toothed (Figs 53, 54) 15
- 14. Labio-maxillary complex elongate; hindwing vein 2-SC+R strongly transverse (Fig. 14) *Calcaribracon* (*Calcaribracon*)
- Labio-maxillary complex normal; hindwing vein 2-SC+R interstitial or longitudinal (see Fig. 101) *Calcaribracon* (*Arostrobracon*)
- 15. Shortest distance between 1st discal cell and 2nd submarginal cell of forewing at least 0.85 times shortest distance between 1st submarginal and 3rd submarginal cell (Fig. 15) *Tropobracon*
- Shortest distance between 1st discal cell and 2nd submarginal cell not more than 0.7 times shortest distance between 1st and 3rd submarginal cells (Figs 16, 17, 87, 89) 16
- 16. Marginal cell of forewing short, vein SR1 reaching wing margin less than 0.65 times the distance between the apex of the pterostigma and the wing tip (Fig. 16); propodeum largely sculptured *Vipiomorpha*
- Marginal cell of forewing longer, vein SR1 reaching wing margin more than 0.8 times the distance between the apex of the pterostigma and the wingtip (Figs 17-19); propodeum often smooth 17
- 17. First metasomal tergite very slender, more than 3.0 times longer than maximally wide (Fig. 70); forewing vein 1-SR+M straight or virtually so; metasoma completely smooth and shiny *Myosoma*
- First metasomal tergite less than 2.5 times longer than maximally wide (see Figs 65-67); forewing vein 1-SR+M straight or curved; metasoma variably sculptured 18
- 18. Forewing vein 1-SR+M strongly curved posteriorly after arising from vein 1-SR (Fig. 17; see also Fig. 91), median flagellomeres shorter than wide; metasoma completely smooth and shiny *Mollibracon*
- Forewing vein 1-SR+M straight or weakly curved (see Figs 12, 13) or if strongly curved (some *Bracon* spp.) then the median flagellomeres are distinctly longer than wide; metasoma variably sculptured 19
- 19. Forewing vein 3-SR more than 1.6 times longer than vein r, usually more than 1.9 times longer (see Figs 87, 88); forewing vein r more or less straight (see Fig. 88) *Bracon* (part)
- Forewing vein 3-SR less than 1.5 times longer than vein r, usually less than 1.2 times (Fig. 86); forewing vein r usually rather sinuous (Fig. 86) *Habrobracon*
- 20. Middle of clypeus strongly produced to form a massive beak-like process (Figs 9, 10) *Psittacibracon*
- Middle of clypeus at most with a lamelliform carina (Fig. 75) 21
- 21. Forewing vein CU1b much wider anteriorly than posterior part of vein 3-CU1 (Figs 21, 22, 94), 1st subdiscal cell being more or less strongly ovoid

- or petiolate (Figs 21, 22, 94) (*Aphrastobraconina* part) 33
- Forewing vein CUIb not or hardly wider than posterior part of vein 3-CUI (Figs 95-100), 1st subdiscal cell not ovoid or petiolate 22
22. Pedicellus large, highly petiolate, medially protruding and with a large but discrete patch of specialized sensillae (Fig. 85); fore tibia with a longitudinal row of thickened, peg-like setae (Fig. 83) *Serratoobracon*
- Pedicellus normal-sized, not petiolate and without a patch of specialised sensillae (if with sensillae then these not restricted to one side of pedicellus) (see Figs 27, 28, 31); fore tibia without a longitudinal row of thickened, peg-like setae 23
23. With a strong spur arising from forewing vein 3-CUI (Fig. 100); transverse median clypeal carina strongly protruding (Fig. 75); forewing vein 1-SR+M moderately curved, not sharply angled (see Figs 21, 26) *Ploceobracon*
- Forewing vein 3-CUI usually without a spur (see Figs 96-99) or if with a spur (e.g. some *Virgulibracon*) then transverse median clypeal carina not strongly produced (see Figs 44-48) and/or forewing vein 1-SR+M sharply angled (Figs 90, 92) 24
24. Ovipositor without a pre-apical dorsal notch or nodus (Figs 128, 130, 131) 25
- Ovipositor with a distinct pre-apical dorsal notch or nodus (see Figs 133-138) 27
25. Ovipositor very short, thick and laterally compressed (Fig. 131), the exerted part shorter than metasomal syntergite 2+3; all metasomal tergites largely smooth and shiny *Stigmatobracon*
- Ovipositor longer and more slender (Figs 128, 130), the exerted part longer than metasomal syntergite 2+3; at least basal 2 metasomal tergites largely coarsely sculptured (Fig. 67) 26
26. First metasomal tergite with a well-developed mid-longitudinal carina (Fig. 67); ovipositor gradually and more or less evenly narrowing from base to apex (Fig. 128); eyes virtually glabrous *Hybaeator*
- First metasomal tergite without a mid-longitudinal carina; ovipositor distinctly deepening pre-apically (Fig. 130); eyes usually setose *Pycnoobraconoides* gen. nov.
27. Forewing vein 1-SR+M sharply and strongly angled posteriorly approximately one third of the distance from its base (Figs 19, 90, 92), often with a distinct spur arising from the angulation (Fig. 92) 28
- Forewing vein 1-SR+M straight or gently and more or less evenly curved posteriorly (see Figs 87, 91, 94, 97), without a spur 30
28. First metasomal tergite with dorsal carina joining dorso-lateral carina (Figs 66, 108); second metasomal tergite with a large well-developed mid-basal, posteriorly narrowing, triangular area (Fig. 66); 3rd metasomal tergite with well-developed antero-lateral, posteriorly diverging grooves; hindwing with a glabrous area distal to vein 1r-m *Vomerobracon*
- First metasomal tergite without dorsal or dorso-lateral carinae (Fig. 65); second metasomal tergite without a posteriorly narrowing, mid-basal triangular area, sometimes with a pair of posteriorly diverging grooves (Fig. 65); 3rd metasomal tergite without, or with only weak, antero-lateral grooves 29
29. Forewing vein r-m with only one bulla (posterior one); antero-lateral areas of 2nd metasomal tergite membranous, unsclerotized *Virgulibracon*
- Forewing vein r-m with two bullae; antero-lateral areas of 2nd metasomal tergite distinctly sclerotized *Virgulibraconoides*
30. Forewing cu-a interstitial or virtually so (see Figs 97-100); lower part of clypeus sharply recessed into the hypoclypeal depression (see Figs 41-43, 47); ovipositor less than 2.5 times longer than forewing; forewing veins C+SC+R and 1-SR forming an angle of more than 50°; base of hindwing usually evenly setose *Bracon* (part)
- Forewing vein cu-a postfurcal, removed from vein 1-M by more than the width of a vein (Figs 20, 96); lower part of clypeus hardly recessed into hypoclypeal depression, the hypoclypeal hair brushes orientated more or less anteriorly (Fig. 48); ovipositor more than 3.5 times longer than the forewing; forewing veins C+SC+R and 1-SR forming an angle of less than 50°; base of hindwing with a large glabrous area 31
31. Hindwing vein 1r-m longer than vein SC+RI (Fig. 20) *Euobracon*
- Hindwing vein 1r-m shorter than SC+RI (see Figs 101, 102) *Euobraconoides*
32. Forewing vein 3-CUI (usually) narrowing posteriorly where it is narrower than the anteriorly thickened vein CUIb (Figs 21, 22, 94); 1st subdiscal cell with a medio-distal glabrous area (Figs 21, 22, 25); forewing vein 2-1A often markedly curved or angled (Fig. 94) (*Aphrastobraconina*) 33
- Forewing vein 3-CUI not markedly narrowed posteriorly and not narrower than vein CUIb (Figs 97-99); 1st subdiscal cell usually evenly setose; forewing vein 2-1A not strongly curved or angled (see Figs 97-99) 39
33. Ovipositor formed into 3 arch-like sections poste-

- riorly (Fig. 125); base of hindwing evenly setose *Undabracoon*
- Ovipositor at most formed into a single distal arch (Figs 123, 124, 126); base of hindwing with a large glabrous area34
34. Ovipositor formed into a single distal arch (Figs 123, 124); fore wing vein r-m with a single posterior bulla (Figs 21, 88)35
- Ovipositor not formed into an arch distally (Fig. 126); forewing vein r-m with two bulli (see Fig. 20) or largely unsclerotized (Fig. 22)36
35. Ovipositor arch shallow, occupying approximately 0.3 of the exerted length of the ovipositor, base of arch indicated by angular expansion of the lower valves (Fig. 123); labio-maxillary complex somewhat elongate *Ligulibracon*
- Ovipositor arch deep, occupying less than 0.2 of the exerted length of the ovipositor, without angular basal projections of the lower valves (Fig. 124); labio-maxillary complex not elongate *Cedilla*
36. Width of head (across eyes)/length of head less than 1.48; face with coarse foveate to rugose sculpture (Fig. 41)37
- Width of head (across eyes)/length of head more than 1.50; face shiny, smooth with scattered punctures (Fig. 43) *Eucurriea*
37. Length of forewing vein 3-SR less than 1.65 times length of m-cu (Fig. 25); 1st tergite with weak dorso-lateral carinae *Vipiellus* (part)
- Length of forewing vein 3-SR more than 1.7 times length of m-cu (Fig. 22); 1st tergite with or without dorso-lateral carinae38
38. First metasomal tergite without dorso-lateral carinae (Fig. 61) *Megalomnum*
- First metasomal tergite with at least a trace of dorso-lateral carinae (see Figs 60, 66, 67) *Curriea*
39. Scapus angularly narrowed basally (petiolate), with a broad preapical concave ledge (Figs 34-36, 39, 80); only ever with one specialized bristle at apex of hindwing vein C+SC+R (Figs 51, 103); pedicellus petiolate, strongly protruding medially with area of specialized sculpture (Figs 34, 35, 37, 38, 80)40
- Scapus not angularly narrowed basally, without such a broad preapical ledge (Figs 29, 32); often with more than one especially thickened seta at apex of hind wing vein C+SC+R (Figs 49, 50); pedicellus more or less parallel-sided or distally narrowing, at most only slightly narrowed basally, not produced medially (Figs 29, 32, 33)42
40. Face with a well-developed, transverse, protruding plate (Figs 39, 40, 44); apico-ventral setae of penultimate tarsal article very long, more than 0.8 times ventral length of telotarsus41
- Face without a plate-like projection (Fig. 77); apico-ventral setae of penultimate tarsal articles much shorter, not more than 0.5 times ventral length of telotarsus (see Figs 53, 55) *Atanycolus*
41. Face with a horn-like, apically truncate projection medially arising from the base of the plate-like projection (Fig. 40) *Chaoilta* (*Blastomorpha*)
- Face at most with a mid-longitudinal, lamelliform carina above the plate-like projection (Fig. 39) *Chaoilta* (*Chaoilta*)
42. Claws bifurcate (Figs 57, 58) *Macrobracon*
- Claws simple (Figs 55, 56)43
43. Length of 1st subdiscal cell (parallel to vein 2-CU1) more than twice width of cell (perpendicular to vein 2-CU1) (Figs 23, 97); forewing vein r-m short, almost entirely unsclerotized, not tubular, without distinct bullae (Fig. 23); ovipositor with at least a weak pre-apical dorsal notch or nodus (Figs 135, 136) *Eunesaulax*
- 1st subdiscal cell less than 1.9 times longer than wide (Fig. 25) or if shorter then either forewing vein r-m longer, largely sclerotized and tubular, often with 1 or 2 distinct bullae (see Figs 20-22, 24-26), or ovipositor without a pre-apical dorsal notch or nodus (Figs 127-132)44
44. Forewing vein 1-SR+M distinctly curving towards the anterior wing margin after arising from 1-SR (Fig. 93; see also Fig. 16); angle between veins 1-SR and C+SC+R less than 50°; forewing vein r more than 0.69 times length of m-cu *Stenobracon*
- Forewing vein 1-SR+M usually distinctly curved posteriorly after arising from 1-SR (see Figs 19-26, 90, 97) or if more or less straight then angle between veins 1-SR and C+SC+R more than 55° and/or vein r less than 0.65 times length of vein m-cu45
45. Ovipositor (part extending beyond apex of metasoma) more than twice length of forewing46
- Ovipositor (part extending beyond apex of metasoma) less than 1.4 times length of forewing47
46. Apex of ovipositor smoothly expanded but without a pre-apical dorsal nodus or apicoventral serrations (Fig. 127); 2nd metasomal tergite smooth (Fig. 106); 3rd metasomal tergite with a medially broken, transverse median groove or a pair of broader depressions (Fig. 106), otherwise smooth and shiny; labio-maxillary complex not elongate; posterior margin of propodeum simple, without carinae *Paramesaulax*
- Apex of ovipositor with a distinct pre-apical dorsal nodus and ventral serrations; 2nd metasomal tergite coarsely sculptured (Fig. 104); 3rd metasoma

- mal tergite without a transverse median groove, largely sculptured; labio-maxillary complex moderately elongate; posterior margin of propodeum with one or more pairs of short, anteriorly diverging carinae *Rostraulax*
47. Ovipositor without a pre-apical dorsal notch or nodus (Fig. 129, also see Fig. 128) 48
- Ovipositor with a pre-apical dorsal notch or nodus (see Figs 133, 134) 49
48. 2nd metasomal tergite with a posteriorly narrowing, mid-basal raised triangular area (see Fig. 60); forewing vein 3-SR less than 1.9 times length of r-m (Fig. 25); posterior margins of metasomal tergites 3-5 membranous, without transverse sub-posterior grooves *Vipiellus* (part)
- 2nd metasomal tergite without a posteriorly narrowing, mid-basal triangular area (Fig. 63); forewing vein 3-SR more than twice length of r-m; posterior margins of metasomal tergites 3-5 sclerotized and convex in lateral profile and with transverse subposterior groove *Iphiaulax*
49. Metasoma short, robust and strongly sculptured (Fig. 62); 3rd metasomal tergite more than 3.75 times wider than minimally long. *Campyloneurus*
- Metasoma moderately elongate and largely smooth and shiny (Fig. 64); 3rd metasomal tergite less than 2.25 times wider than minimally long *Callibracon*

NOTES ON THE AUSTRALIAN GENERA INCLUDING DESCRIPTIONS OF A NEW GENUS AND NEW SPECIES

New records for genera occurring in Australia are indicated by an asterisk. Full details of synonymy are given in Shenefelt (1978), Quicke (1987b, 1991a) and Quicke & van Achterberg (1990).

**Acrocerilia* van Achterberg

Previously known only from the type species, *A. pachynervis* van Achterberg, from the Philippines where it has been reared from the gracilariid cocoa moth, *Acrocercops cramerella* Snellen. The biological details available for this species indicate that it emerges from the prepupa of its host and therefore van Achterberg (1989) cautiously suggested that it might in fact be an endoparasitoid though precise data are lacking. In terms of its relationships, *Acrocerilia* appears intermediate in structure between certain genera of the *Plesiobracon* group, in particular *Psilolobus* van Achterberg and *Simplicibracon* Quicke, and members of the *Aspidobraconina*

(see *Hyboteles* van Achterberg and *Pedinopleura* van Achterberg). If an association with the *Aspidobraconina* which are endoparasitoids of butterfly pupae is proven then this would add some support to the possibility that *Acrocerilia* might also be endoparasitic.

Key to species of *Acrocerilia*

1. Top of head coriaceous; head black and white; metasoma dorsally black with a white margin; hindwing vein 1-M narrowing distally *A. tricolor* sp. nov.
- Top of head smooth; head brownish yellow; metasoma entirely brownish yellow; hindwing vein 1-M uniformly broad along its whole length *A. pachynervis* van Achterberg

Acrocerilia tricolor sp. nov.

MATERIAL EXAMINED

HOLOTYPE: ♂ labelled: 'AUSTRALIA NE Queensland Conway Range Nat. Park E from Proserpine' and 'No. 226, 22.II.1981 leg. Hangay and Vojnits at light'. Deposited in QMBA.

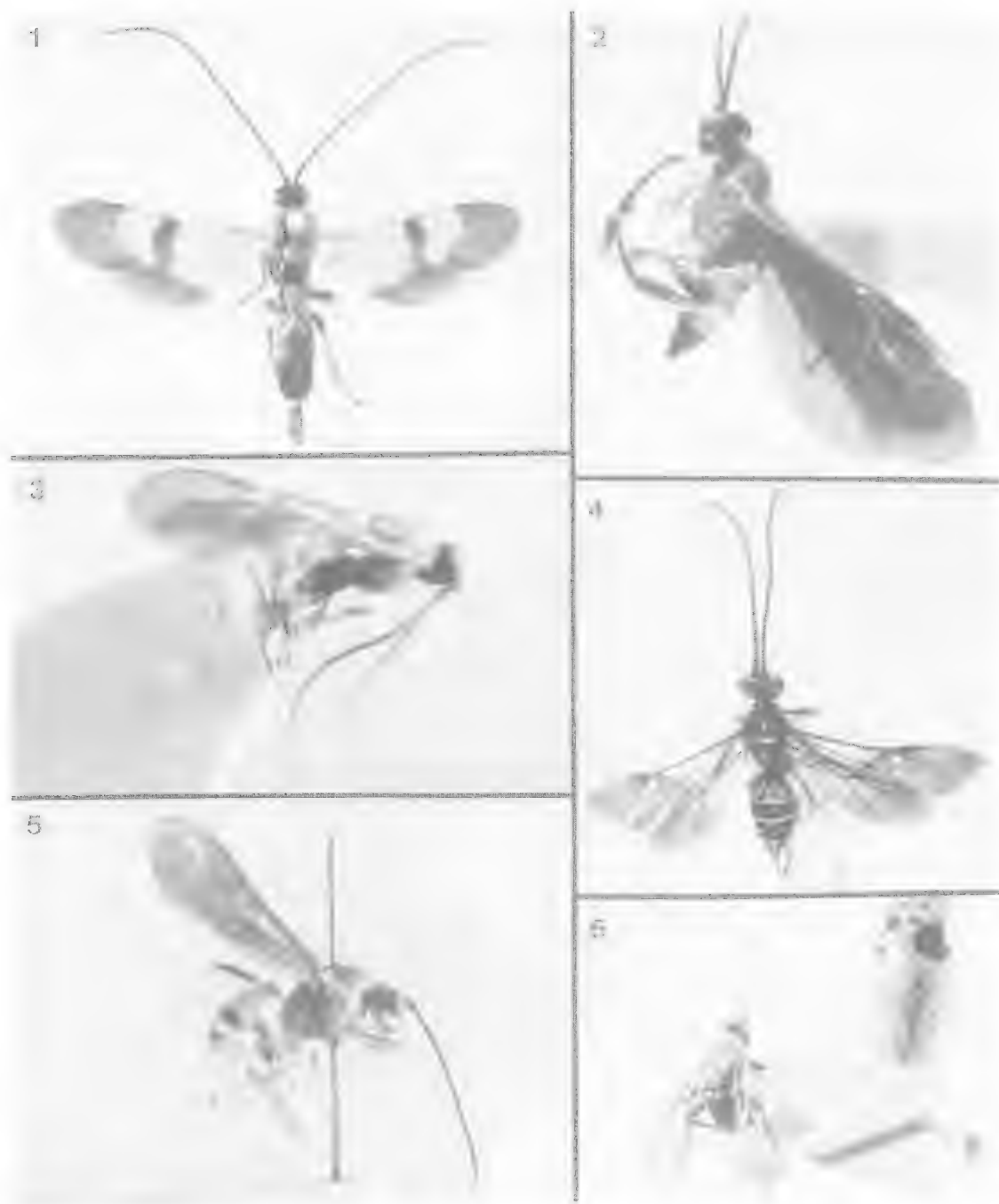
PARATYPE: ♂ labelled: 'AUSTRALIA NE Queensland Conway Range Nat. Park E from Proserpine' and '18.II.1981 No. 177 leg. Hangay and Vojnits, at light'. HNHM.

DESCRIPTION (♂ ♂)

Length of body 4.4-5.0mm, of forewing 4.0-4.5mm and of antenna 4.6-5.0mm.

Antennae with 43-44 flagellomeres. Terminal flagellomere acuminate. First flagellomere 1.07 and 1.15 times longer than the 2nd and 3rd respectively, the latter being 1.5 times longer than wide. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0: 3.8: 2.9. Height of eye: shortest distance between eyes: width of head = 1.0: 1.29: 2.37. Width of face: height of face = 2.05: 1.0. Face except for supra clypeal triangle densely, finely punctate, the punctures being arranged in transverse rows giving the face a striate appearance. Eyes virtually glabrous. Frons, temples and occiput coriaceous, back of head becoming finely striate. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.25: 1.0: 2.25. Horizontal length of eye: horizontal length of head behind eye = 2.85: 1.0.

Mesosoma 1.48 times longer than maximally high. Pronotum with crenulate groove laterally. Notauli moderately well-developed on anterior



FIGS 1-6. 1. *Stigmatobracon diversipennis* Turner, ♀. 2. *Myosoma rufescens* sp.nov., ♂ paratype. 3. *Trigastrotrothea tricolor* sp.nov., ♀ paratype. 4. *Virgulibraconoides* sp., ♀. 5. *Simplicibracon nigratarsus* sp.nov., ♀ holotype. 6. *Pycnobraconoides mutator* (Fabricius) comb. nov., ♀ and host cocoon with parasitoid's emergence hole.

half of mesoscutum, absent on posterior half. Scutellar sulcus with 5 transverse crenulae. Mesoscutum, scutellum, mesopleuron and mesosternum densely and evenly setose, punctulate. Precoxal suture indicated by a weak depression. Mesopleural suture punctate. Median area of metanotum with a short carina anteriorly; merging with a flat triangular plate posteriorly in one specimen. Propodeum with a complete mid-longitudinal carina bordered by crenulae; posterior margin with numerous strong crenulations merging into rugose sculpture on the posterior half of the propodeum.

Forewing. Pterostigma 2.8 times longer than maximally wide. Lengths of veins SR1: 3-SR:r = 5.0: 1.6: 1.0. Lengths of veins 2- SR:3-SR:r-m = 1.36:1.36:1.0. Vein 2-M curved. Vein 1-M straight. Vein 1-SR forming an angle of approximately 80°. Veins cu-a more or less interstitial.

Hindwing. Vein 1r-m 0.35 times length of SC+R1. Apex of C+SC+R with one especially thickened bristle. Vein 2-1A absent. Base of discal + subdiscal cell with a large glabrous area.

Lengths of fore femur: tibia: tarsus = 1.0: 1.13: 1.20. Lengths of hind femur: tibia: basitarsus = 2.0: 2.7: 1.0. Hind tibia slender, maximally deep at apex. Hind basitarsus 5 times long than deep.

Metasomal tergites 1-5 largely foveate-rugose. Second tergite 2.0 times wider than medially long. Second suture crenulate, moderately curved. Tergites 3-5 with well-developed, anterolateral areas. Posterior margin of 5th tergite slightly irregular.

Head ivory-white except for tips of mandibles, a triangular mark above the clypeus and the frons, temples, occiput and back of head down to level of base of eye which are black. Mesosoma brownish orange except for propodeum which is largely piceous. Fore and middle legs brownish orange, hind legs piceous to black. Metasomal tergites black except for the following which are ivory-white: the base and lateral margins (broadly) of the 1st tergite, the lateral margins of tergites 1-5 (narrowly) and their antero-lateral triangular areas, and the posterior margin of the 5th tergite. Wings uniformly very pale brown with dark brown pterostigma and venation.

**Africadesha* Quicke

Members of the Adeshini, these small wasps have wing lengths less than 3mm. *Africadesha* is previously known from a single Afrotropical species, *A. usherwoodi* Quicke, though several other undescribed Afrotropical species have been seen

by the senior author. Despite the strange disjunct distribution indicated by the discovery of the new Australian species, the two species differ only in relatively small characters and there is no reason to doubt the two as being anything other than congeneric. Nothing is known of the biology of any of the Adeshini. Further, given their small size, it is quite likely that members of other genera of this tribe will be found in Australia and the reader is referred to van Achterberg (1983a) and Quicke (1986b, 1988f).

Key to species of *Africadesha*

1. First metasomal tergite more than 1.5 times longer than posteriorly wide; third metasomal tergite with well-developed longitudinally striate sculpture (Fig. 109) *A. tobiasi* sp. nov.
- First metasomal tergite less than 1.4 times longer than posteriorly wide; third metasomal tergite without longitudinally striate sculpture
..... *A. usherwoodi* Quicke

Africadesha tobiasi sp. nov.

(Figs 12, 109, 134)

MATERIAL EXAMINED

HOLOTYPE: ♀ labelled: '15 km NE Kuranda, Queensland, 1.V-14.VI. 1985 MDPI FIT site 25, Storey & Halfpapp', Deposited in QMBA.

PARATYPES: 3 ♀ ♀, same data as holotype. QMBA, QDPI and BMNH.

DESCRIPTION (♀ ♀)

Length of body 2.7mm, of forewing 2.6mm, of ovipositor (part exerted beyond apex of metasoma) 0.45mm and of antenna 4.2mm.

Antenna with 42 flagellomeres, considerably longer than the body. Terminal flagellomere pointed but not acuminate, 2.3 times longer than wide. Median flagellomeres 1.7 times longer than wide. First flagellomere 1.17 and 1.4 times longer than the 2nd and 3rd flagellomeres respectively, the latter being 2.25 times longer than wide. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0:2.8:2.2. Face, frons and occiput coriaceous. Height of eye: shortest distance between eyes: width of head = 1.0:1.375:2.5. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.5:1.0:3.5.

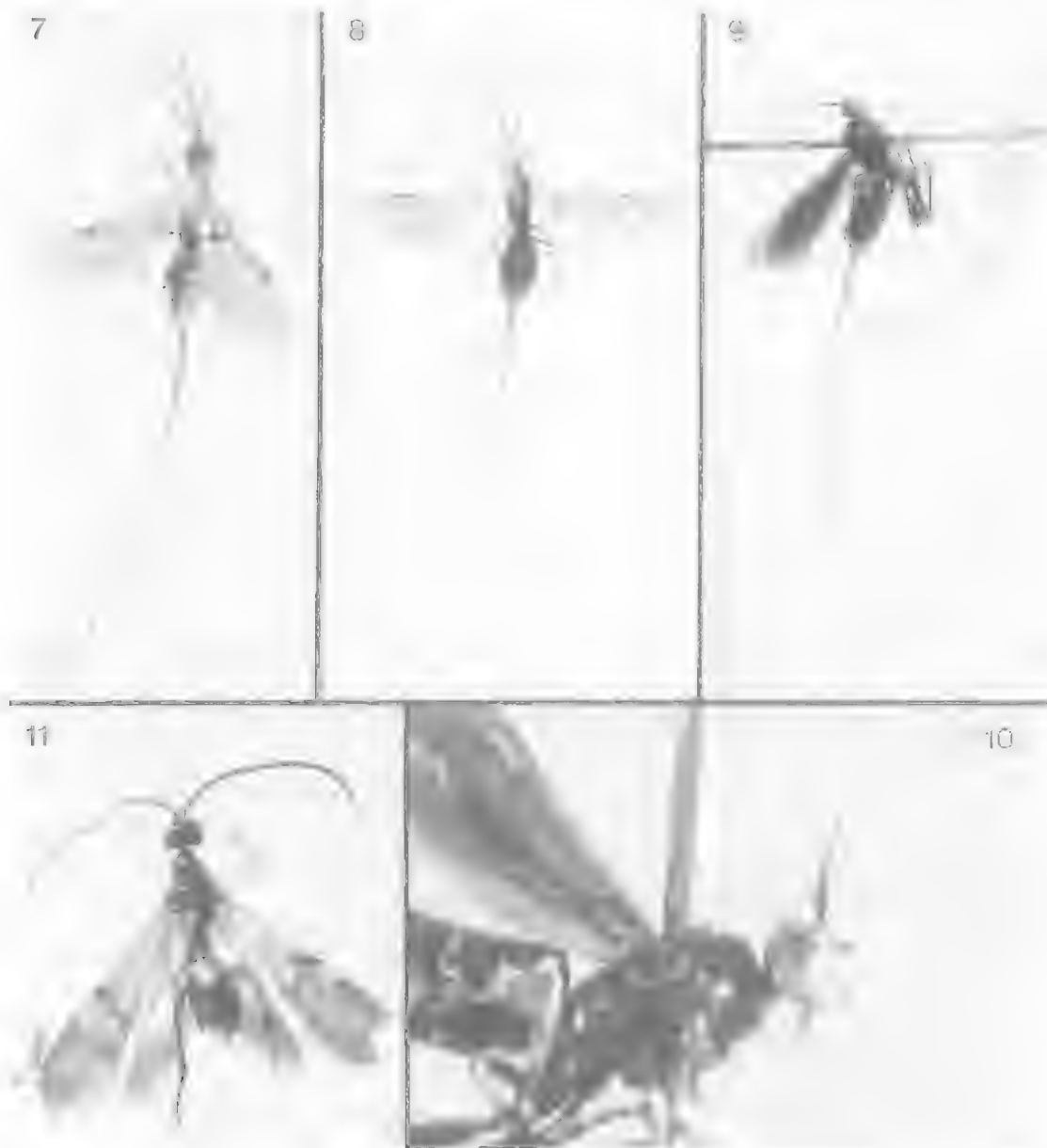
Mesosoma 1.5 times longer than high; largely coriaceous but mesosternum largely smooth and shiny. Precoxal suture very weakly, broadly im-

pressed. Mesopleural suture smooth. Propodeum with a complete mid-longitudinal carina.

Forewing. Lengths of veins SR1: 3-SR:r = 6.7:2.2:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.7:2.0:1.0. Vein 2-SR+M moderately long; shortest distance between 1st subdiscal cell and 2nd submarginal cell: length of vein m-cu = 1.0:1.25. Veins cu-a and 3-CU1 both more or less interstitial.

Lengths of fore femur: tibia: tarsus = 1.0: 1.2: 1.53. Lengths of hind femur: tibia: basitarsus = 1.47: 2.3: 1.0. Hind basitarsus 10 times long than deep.

First tergite 1.8 times longer than posteriorly wide; with rugose sculpture and with thin irregular mid-longitudinal carina. Second tergite 1.2 times wider posteriorly than medially long. Second and 3rd tergites with strong longitudinal



FIGS 7-11. 7. *Eunesaulax terebratus* Tobias, ♀. 8. *Eutrobraconoides longicaudis* Quicke, ♀. 9, 10. *Psittacobracon lacteolus* Quicke, ♀. 11. *Calcaribracon willani* sp.nov., ♀ holotype.

striations (Fig. 109) interspersed with punctate sculpture. Tergites 4 and 5 with fine rugulose to coriaceous sculpture. Fifth tergite without postero-lateral emarginations. Ovipositor (exserted part) about as long as the 5th tergite; with a distinct pre-apical dorsal nodus, apico-ventrally virtually smooth (Fig. 134).

Uniformly pale brownish yellow, flagellum becoming piceous beyond middle, ovipositor sheaths black. Wings weakly infusate with brown venation.

ETYMOLOGY

Named after our esteemed colleague Vladimir Tobias of the Russian Academy of Science, St Petersburg, who drew our attention to many interesting Australian Braconinae.

**Atanycolus* Foerster
(Figs 77, 80, 82, 84, 103)

Synonyms. *Coelobracon* Thomson; *Melanobracon* Ashmead; *Atanycolidae* Viereck.

A widespread genus of medium-sized wasps, commonest in the Nearctic and Palearctic though with some closely related and more derived groups occurring in the neotropics (e.g. *Hemibracon* Szépligeti) and Indo-Australian region (*Nedinoschiza* Cameron). *Nedinoschiza*, which is probably only a specialized derivative of *Atanycolus*, has not yet been recorded from Australia though it may occur there; it can be distinguished from *Atanycolus* by the greatly enlarged anterior tentorial pits. (Quicke, 1987 b)

Atanycolus tomentosus Szépligeti, previously placed in the Braconinae (see Parrott, 1953), is in fact a member of the Doryctinae (Quicke, 1984).

Atanycolus australiensis sp. nov.
(Figs 77, 80, 82, 84)

MATERIAL EXAMINED

HOLOTYPE ♀ with the following label: 'Australia 35-40 km NO Deniliquin, Tobias 12-13.iv.1978'. Deposited in ANIC.

DESCRIPTION (♀)

Length of body 3.9mm, of forewing 3.8mm, of ovipositor (part exserted beyond apex of metasoma) 3.3mm and of antenna 3.0mm.

Antennae (broken) with at least 29 flagellomeres, all flagellomeres longer than wide. First flagellomere 1.25 and 1.5 times longer than 16 2nd and 3rd respectively, the latter being 1.75 times longer than apically wide. Height of eye:

shortest distance between eyes: width of head = 1.1: 1.0:2.1. Face shiny, weakly at and with many deep punctures at the bases of the silvery setae. Eyes sparsely setose; emarginate opposite antennal sockets. Head very elongate (Fig. 77); length of head behind eye: horizontal length of eye = 1.0:1.0. Ocelli small; distance between posterior ocelli; transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 2.0: 1.0: 4.0.

Mesosoma 2.0 times longer than maximally high. Antescutal depression well-developed. Scutellar sulcus shallow with few weak punctures. Scutellum protruding in profile.

Forewing. Lengths of veins SR1: 3-SR: r = 5.3: 2.85: 1.0. Lengths of veins 2-SR: 3-SR: r-m = 1.56: 2.5: 1.0. Vein r-m largely unsclerotized. Vein 1-SR+M rather strongly curved. Veins C+SC+R and 1-SR forming an angle of approximately 80°. Vein cu-a interstitial. Vein CU1b almost as long as 3-CU1.

hindwing. Vein C+SC+R very thick, apex with a single, very large, specialized catch bristle (Fig. 103). Base of wing evenly setose.

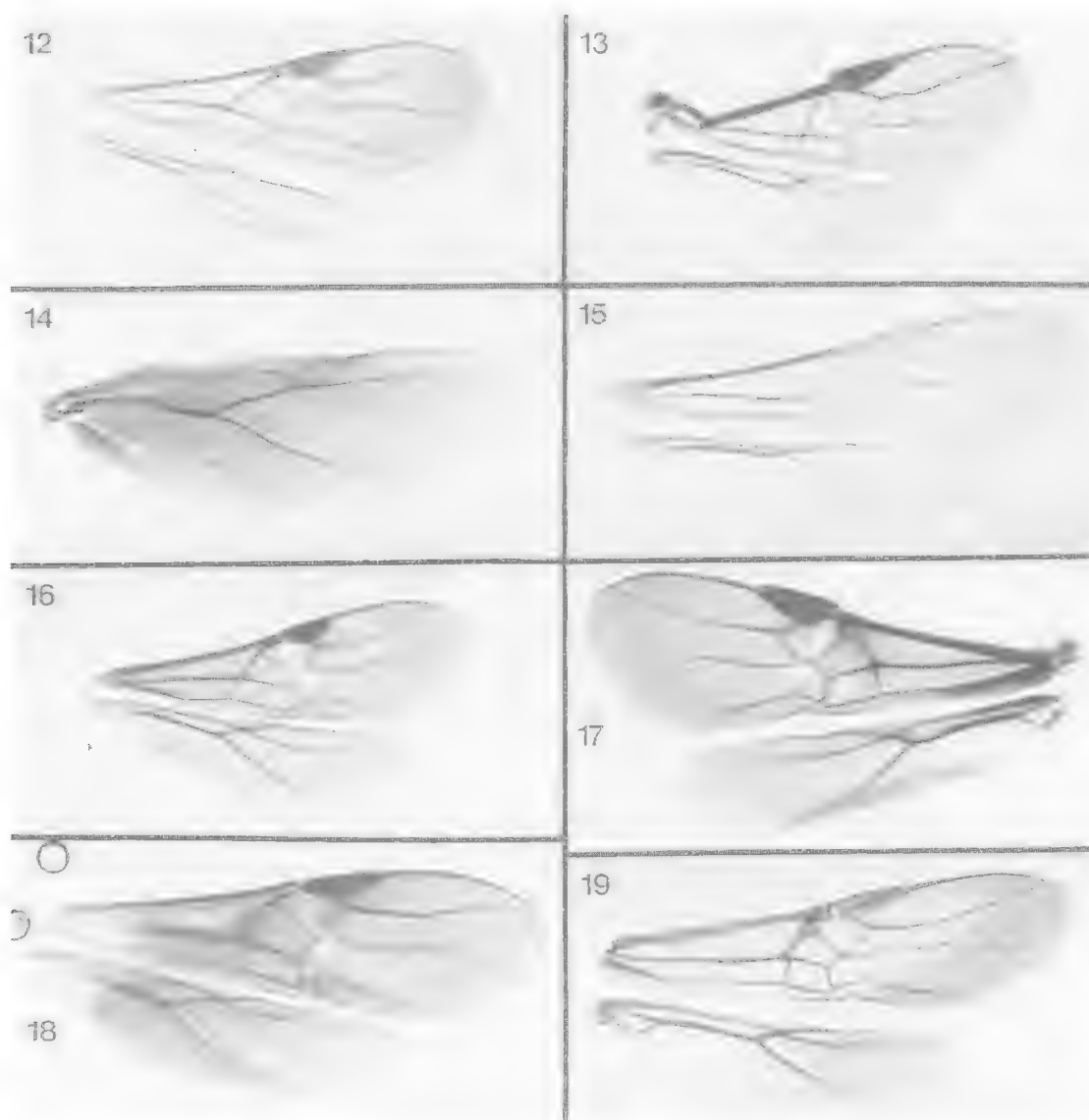
Fore tibia with a well-developed longitudinal row of pegs (Fig. 82). Length of fore femur: tibia: tarsus = 1.0: 1.16: 1.45. Length of hind femur: tibia: basitarsus = 1.95: 2.9: 1.0.

Metasoma largely smooth and shiny. First tergite more or less parallel-sided; raised median area with weak irregular, longitudinal striate sculpture. Second tergite 1.62 times wider than medially long; with a large, acute, triangular mid-basal area bordered on each side by a finely crenulate groove; with sub-lateral, curved, longitudinal, finely crenulate grooves. Second suture sinuous, crenulate. Third tergite with well developed antero-lateral areas. Tergites 3-6 smooth and shiny, without transverse sub-posterior grooves, with posterior margins membranous. Ovipositor (exserted part) approximately 0.85 times length of forewing.

Largely piceous brown except following: head orange-yellow; mesosoma and tergites 5-7, black; posterior (membranous) margins of tergites 4-6 ivory white. Wings light brown with darker brown venation.

Bracon Fabricius
(Figs 51, 53)

Synonyms. *Microbracon* Ashmead; *Amicoplidea* Ashmead; *Macrodyctium* Ashmead; *Tropidobracon* Ashmead; *Liobracon* (Ashmead) Nason; *Seliodus* Brethes.



FIGS 12-19. Wings: 12, *Africadesha tobiasi* sp.nov., ♀ paratype; 13, *Trigastrotheca* sp., ♀ (African species); 14, *Calcaribracon* (*Calcaribracon*) *diores* (Cameron); 15, *Tropobracon* sp., ♀ (African species); 16, *Vipiomorpha ypsilon* Tobias, ♀ (Russian specimen); 17, *Mollibracon bimar*is (Turner), ♀; 18, *Hybogaster* sp., ♀ (Papua New Guinea specimen); 19, *Virgulibracon endoxylaphagus* sp.nov., ♀.

A vast cosmopolitan genus of small wasps which parasitize a wide range of other insects (Quicke, 1988b). Concealed Lepidoptera larvae are the commonest hosts followed by Coleoptera, Diptera, and Hymenoptera-Symphyta (e.g. Austin & Faulds, 1989); in Australia, gall forming Homoptera also appear to be attacked (Chadwick & Nikitin, 1975) but this record should be checked by careful observa-

tion of larval feeding habits. To date only approximately twenty species have been recorded from Australia (Parrot, 1953; Austin & Faulds 1989). However, this is a considerable underestimate and the true number of Australian species is probably in the hundreds. The genus occurs throughout Australia and is morphologically rather diverse there with some distinctive species groups.

Calcaribracon Quicke
(Figs 11, 14, 27, 52, 91, 95)

A small genus ranging from Queensland through New Guinea, Indonesia and Malaysia to SE China and Japan. Keys to the species have been provided by Quicke (1986a, 1988d). Three species are known from Australia, all from Queensland, viz. *C. (Arostrobracon) walkeralis* (Shenefelt), *C. (Arostrobracon) diores* (Cameron) and *C. (Arostrobracon) willani* sp.nov. The Australian specimen of *C. diores* examined differs from the New Guinea specimens in the colour of the hind coxa and femur (yellow not black) and in having forewing vein cu-a less strongly curved. Thus it may in future be found to represent a further new species. We have also included the nominal subgenus in the generic key presented here though all known members of that group have a more northerly distribution (Papua New Guinea to China and Japan). Nothing is known of the biology of the Australian members of this genus but one Japanese species has been reared from larvae of members of the sesiid moth genus *Paranthrene* (Mactô, 1992), while a specimen of *C. ferax* (Smith) from Papua New Guinea in the BMNH has a label 'reared ex cerambycid larva' (Quicke, 1986a); while the former record is definitely correct and agrees better with the known hosts of the related genus *Myosoma* (Quicke, 1989c), the latter record could be erroneous.

Key to Australian species of *Calcaribracon*

1. Pterostigma, base of forewing vein r (usually), and 2nd metasomal tergite largely yellow or orange-yellow (Fig. 11); basal fifth to half of forewing yellow (Fig. 11) 2
- Pterostigma, forewing vein r and 2nd metasomal tergite entirely piceous brown or black; forewing uniformly dark brown *C. diores* (Cameron)
2. Propleuron, propodeum, mid-legs, hind femur, median area of 1st metasomal tergite, metasomal tergites 3-7 piceous or black (Fig. 11); basal half of forewing yellow *C. willani* sp.nov.
- Mesosoma and metasoma up to the 7th tergite, midlegs and hind leg except apex of tibia and tarsus, yellow or orange-yellow; forewing with only basal half of basal and sub-basal cells yellow *C. walkeralis* (Shenefelt)

Calcaribracon (Arostrobracon) willani
sp.nov. (Figs 11, 52, 91)

MATERIAL EXAMINED

HOLOTYPE: ♀ with the following label: 'Zillmere Brisbane, Q. 27 August 1988 G.V. Maynard'. Deposited in QMBA.

DESCRIPTION (♀)

Length of body 8.3mm, of forewing 8.8mm, of ovipositor (part exerted beyond apex of metasoma) 1.1mm and of antenna 8.0mm.

Antenna with 65 flagellomeres. Terminal flagellomere acuminate, 1-8 times longer than maximally wide. Penultimate flagellomere 1.25 times longer than wide. Median part of flagellum rather flattened, median flagellomeres at their widest approximately 1.6 times wider than long. First flagellomere 1.7 times longer than both the 2nd and 3rd separately, the latter being 1.2 times wider than long. Height of eye: width of face: width of head = 1.1:1.0:2.0. Eyes sparsely setose. Lateral half of frons moderately densely with short erect setae. Horizontal length of head behind eye: horizontal length of eye = 1.0:1.37.

Mesosoma 1.7 times longer than high. Mesoscutum almost totally glabrous.

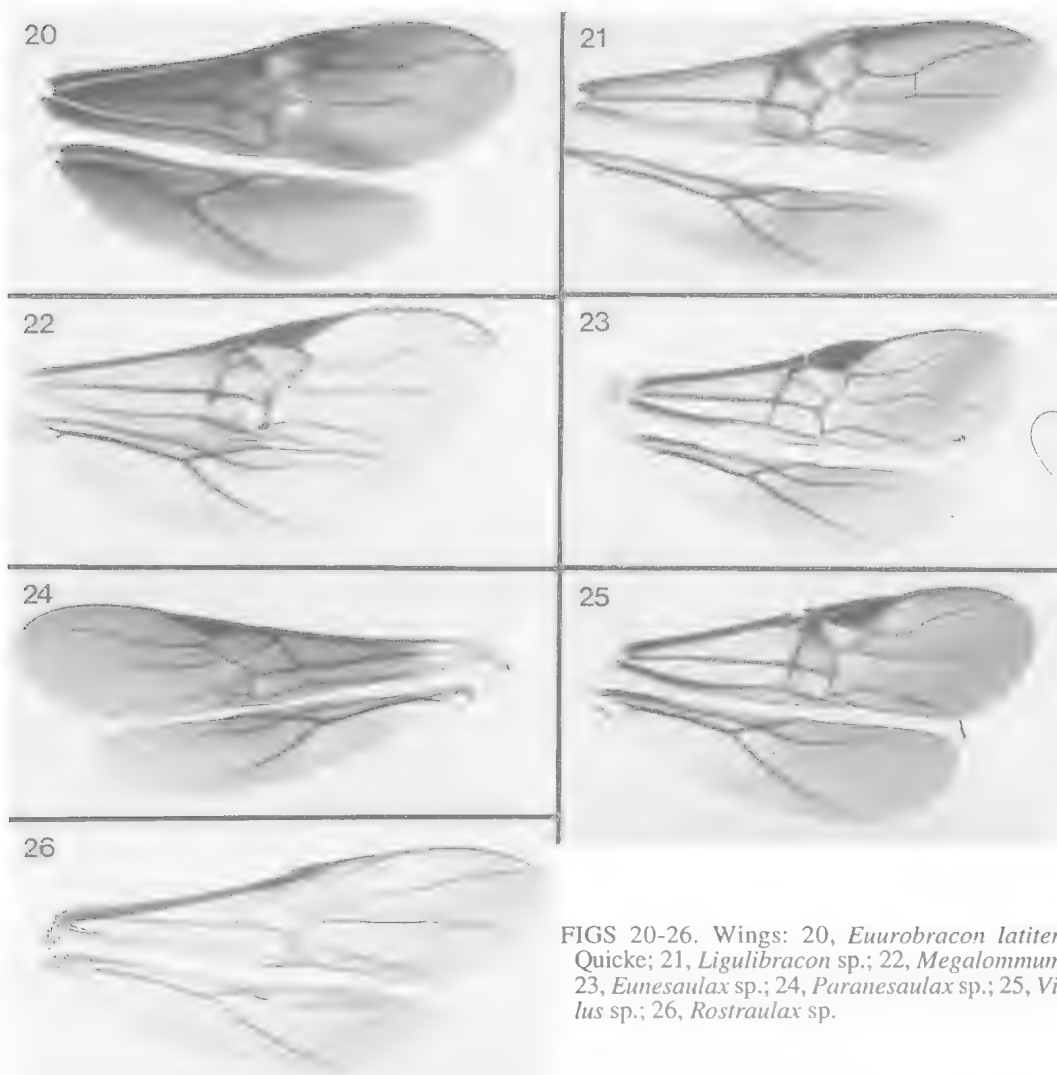
Forewing. Lengths of veins SR1:3-SR:r = 3.5:2.2:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.37:2.2:1.0. Vein r-m with 2 distinct bulli. Vein cu-a antefurcal, strongly bent.

Hindwing. Lengths of veins 1r-m : SC+R1 = 1.05:1.0. Apex of vein C+SC+R with one especially thickened bristle. Vein 2-CU almost reaching wing margin.

Lengths of fore femur: tibia: tarsus = 1.0:1.13:1.33. Lengths of hind femur: tibia: basitarsus = 2.3:2.8:1.0. Hind basitarsus 3.3 times longer than deep.

First metasomal tergite approximately 2.0 times longer than maximally wide, flattened lateral areas of tergum virtually absent sub-posteriorly. Ovipositor (part exerted beyond apex of metasoma) 1.5 times longer than hind basitarsus; 0.1 times length of forewing.

Black except the following which are bright orange-red: pronotum (largely), mesoscutum, scutellum mesopleuron, mesosternum, tegulae, metanotum, posterior of propodeum, apex of fore femur, fore tibia (except spur), fore tarsus, lateral areas of 1st metasomal tergite and 2nd metasomal tergite. Forewing yellow basally, brown apically with yellow pterostigma (Fig. 11).



FIGS 20-26. Wings: 20, *Euurobracon latitempus* Quicke; 21, *Ligulibracon* sp.; 22, *Megalommum* sp.; 23, *Eunesaulax* sp.; 24, *Paranesaulax* sp.; 25, *Vipielus* sp.; 26, *Rostraulax* sp.

ETYMOLOGY

Named after Richard Willan for his kindness and help during DLJQ's visit to Australia.

Callibracon Ashmead (Figs 50, 64)

Synonyms. *Poecilobacon* Cameron syn.nov.

This is a vast, mostly Australian genus of medium-sized to large (and often common) braconines that are greatly in need of taxonomic revision. Previously species were often referred to under the genus *Ipobracon* Thomson (a junior synonym of *Cyanopterus* Haliday). Species have been reared from a variety of wood-boring,

coleopterous hosts including Elateridae and Scolytidae, and three species have been collected in association with *Eucalyptus* infested with the cerambycid genus, *Phoracantha* (Quicke, 1989c; Quicke et al., 1992). Some species are gregarious parasitoids.

The genus *Poecilobracon* Cameron (type species: *Poecilobracon flaviceps* Cameron 1901: 122) is treated here as a new subjective synonym of *Callibracon* since examination of a large number of specimens has shown that the characters used by Quicke (1987b) to distinguish between these, viz. scapus length and metasomal sculpture, show great variation and cannot therefore be used as generic characters.

Campyloneurus Szépligeti
(Fig. 62)

Synonyms. *Monolcia* Enderlein; *Diolcia* Enderlein.

A medium-sized genus of small to medium-sized wasps which are found from India and Japan to Australia. Several species are reported from Australia (Parrott, 1953) but only two appear to be common. Several Australian species included under *Campyloneurus* in the past are referable to *Pycnobraconoides* gen.nov. Australian species of *Campyloneurus* species appear to be largely or perhaps exclusively parasitoids of cerambycid larvae, one Australian species having frequently been reared from members of the cerambycid beetle genus *Zygrita* on a variety of legumes including soya-bean. However, there is a record from grass tree (*Xanthorrhoea*) stems that were infested with both Curculionidae and Cerambycidae. Two host records from India suggest that elsewhere *Campyloneurus* spp. may also attack stem-boring pyralid moth larvae (Quicke, 1989c). The available evidence suggests that at least some species are gregarious parasitoids.

Cedilla Quicke
(Figs 94, 124)

Known from only a single Australian species of medium-sized Aphrastobraconini (Quicke & Tobias, 1990). Nothing is known of its biology though the type specimen of the type species was collected at light indicating that they may be crepuscular or nocturnal as appears to be commonly the case with Australian Aphrastobraconini (Quicke, 1992).

Chaoilta Cameron
(Figs 34, 35, 36, 37, 38, 39, 40, 44, 69)

Synonyms. *Blastomorpha* Szépligeti; *Platybracon* Szépligeti; *Iphioilta* Ramakrishna Ayyar.

A rather small genus of medium-sized to large braconines. Distributed from India to Australia, most species have been described from Indonesia and New Guinea. The five Australian species were treated by Quicke (1991a); *C. (Blastomorpha) decorata* Szépligeti is restricted to north Queensland the other four species belonging to the nominal subgenus are more widespread. Nothing is known of the biology of *Chaoilta*. However, the closely related genera *Atanycolus* Foerster, principally from the Holarctic, and *Odontoscopus* Kriechbaumer from the Afrotropical Region are both parasitoids of bark-boring

coleopterous larvae, particularly of the families Bostrychidae and Buprestidae (Quicke, 1988b, 1989c).

Curriea Ashmead

A small genus of the tribe Aphrastobraconini originally described from the Afrotropical Region but widespread through the Old World tropics and recorded from Australia for the first time by Quicke (1992). We have seen several Australian species, all of which appear to be undescribed.

Esengoides Quicke

A small genus of the tribe Braconini known from only two species: *E. fulvus* Quicke from Australia (north Queensland) and *E. crenulatus* Quicke from the Solomon Islands (Quicke, 1989b). Small wasps with wing lengths less than 5mm. Nothing is known of their biology.

Eucurriea Quicke
(Figs 28, 31, 43)

A small genus of medium-sized wasps previously confused with *Megalommum* and *Curriea* Ashmead (see Quicke & Tobias, 1990). Frequently collected at light (Quicke, 1992); nothing else is known of their biology.

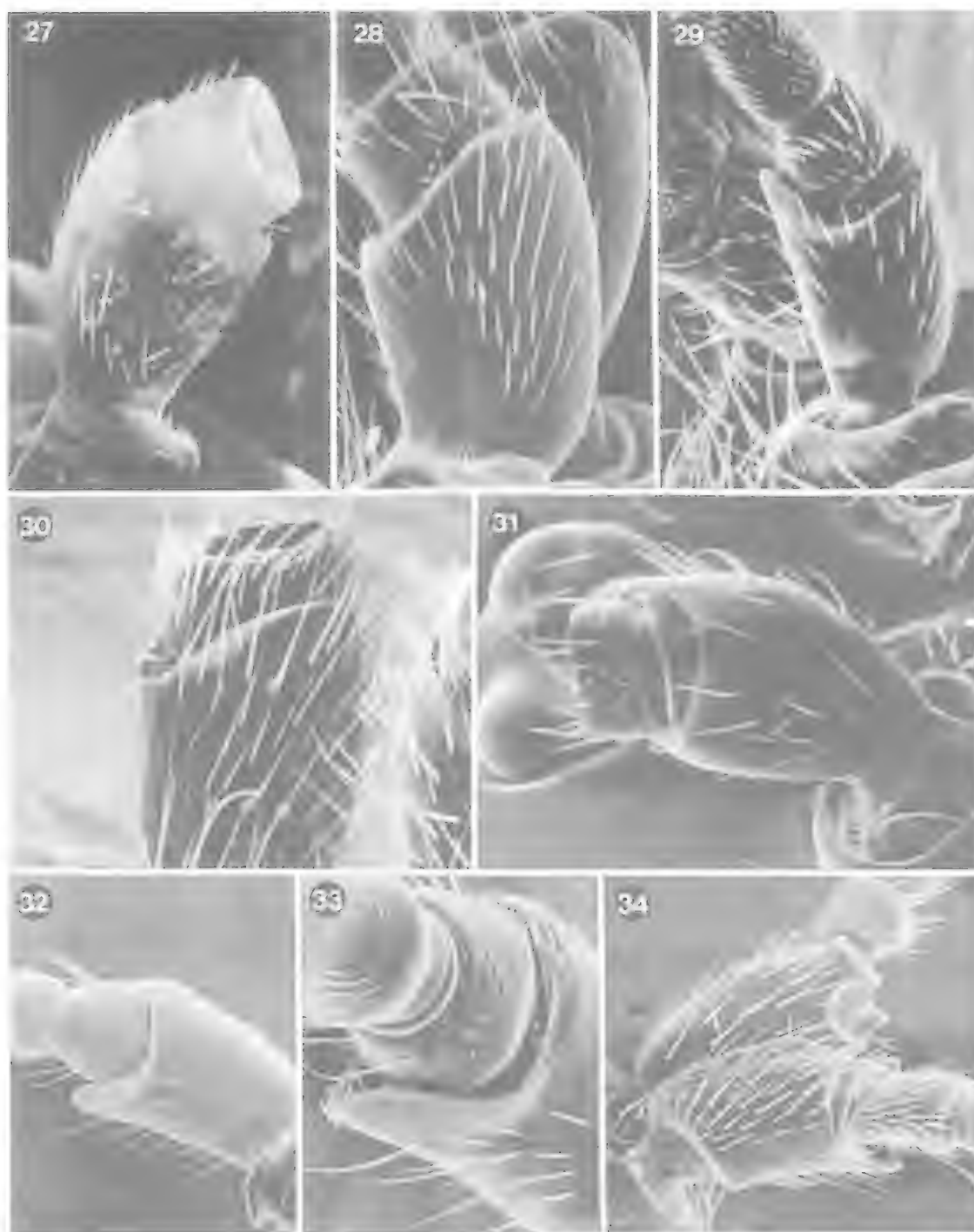
Eunesaulax Tobias
(Figs 7, 23, 60, 68, 135, 136)

A small genus of medium-sized rather slender wasps, known from three Australian species, *E. terebratus* Tobias, *E. nigriventris* Tobias and *E. radialis* Tobias (Quicke & Tobias, 1990). The wing venation is fairly distinctive but the form of the ovipositor apex shows considerable variation (Fig. 135 cf. 136). Nothing is known of their biology and their relationships are still uncertain.

Euurobracon Ashmead
(Figs 20, 48, 56, 96)

Synonyms. *Delmira* Cameron; *Exobracon* Szépligeti; *Lissobracon* Cameron.

It is not known for certain whether this genus occurs in Australia. A single specimen of *E. latitempus* Quicke was found in a Queensland collection but it lacked data (Quicke, 1989a). However, as *Euurobracon* occurs in Papua New Guinea it is quite likely that it also occurs at least



FIGS 27-34. Features of scapus and pedicellus: 27, *Calcaribracon* sp., medial aspect; 28, *Eucurriea* sp., lateral aspect; 29, *Ligulibracon* sp., lateral aspect; 30, *Hybogaster* sp., ventro-medial aspect; 31, *Eucurriea* sp., medial aspect; 32, *Iphiaulax* sp., lateral aspect; 33, *Iphiaulax* sp., apico-ventro-medial aspect; 34, *Chaoilta* (*Chaoilta*) sp., lateral and medial aspects.

in far north Queensland. *Euurobracon* species are large wasps, sometimes with extremely long ovipositors (van Achterberg, 1986; Quicke, 1987b), and they have been reared from cerambycid beetle larvae living deep within wood (Quicke, 1989c).

***Euurobraconoides* Quicke**
(Fig. 8)

Medium-sized braconines belonging to the tribe Euurobraconini with wing-lengths between 9 and 11mm. Known from a single Australian (north Queensland) species, *E. longicaudis* Quicke (Fig. 8). Nothing is known of its biology (Quicke, 1988c) but one specimen is labelled as having been collected in rainforest.

****Furcadesha* Quicke**

Small wasps belonging to the Adeshini. Known only from the type species *F. huddlestoni* from India and *F. walteri* sp.nov. from south-west Queensland. Nothing is known of the biology of any of the Adeshini though both *F. walteri* and the new *Africadesha* (q.v.) species described above were collected by vacuum suction from grass and low herbs.

Key to species of *Furcadesha*

1. Forewing vein SR1 more than 2.4 times longer than vein 3-SR; lateral lobes of mesoscutum extensively setose; mesosoma and metasomal tergites extensively marked with black*F. huddlestoni* Quicke
- Forewing vein SR1 less than 1.8 times longer than vein 3-SR; lateral lobes of mesoscutum largely glabrous except postero- medially and along line of notaulus; mesosoma and metasoma entirely brownish yellow to brownish orange*F. walteri* sp.nov.

***Furcadesha walteri* sp.nov.**

(Figs 81, 89, 110, 111)

MATERIAL EXAMINED

HOLOTYPE: ♀ with the following labels: 'MT. Nebo, S.E. Queensland, 1.IV, 1974 I.D. Galloway' and 'CAUGHT USING D- VAC SUCTION NET'. Deposited in QMBA (originally from QDPI).

DESCRIPTION (♀)

Length of body 3.1mm, of forewing 3.1mm and

of ovipositor (part exerted beyond apex of metasoma) 0.3mm.

First flagellomere 1.25 times longer than the 2nd. Scapus normal, not expanded dorsally. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0:1.6:1.35. Height of eye: width of face: width of head = 1.0:1.35:2.5. Face smooth. Horizontal length of eye: horizontal length of head behind eye = 2.8:1.0. Head strongly narrowed behind eye. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.6:1.0:3.3.

Mesosoma 1.65 times longer than high. Mesoscutum setose medio- posteriorly and along lines of notauli. Notauli deeply impressed, minutely crenulate. Medio-posterior part of mesoscutum rugose, otherwise mesoscutum smooth and shiny. Precoxal suture virtually absent, mesopleuron and mesosternum largely smooth and shiny.

Forewing. Lengths of veins SR1:3-SR:r = 7.25:4.5:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.1:2.0:1.0. Vein 2-SR+M short; shortest distance between 1st subdiscal cell and 2nd submarginal cell: length of vein m-cu = 1.0:2.7. Vein cu-a interstitial. Vein 3-CU1 slightly postfurcal with respect to m-cu.

Base of hindwing evenly setose. Posterior margin of hindwing distinctly emarginate.

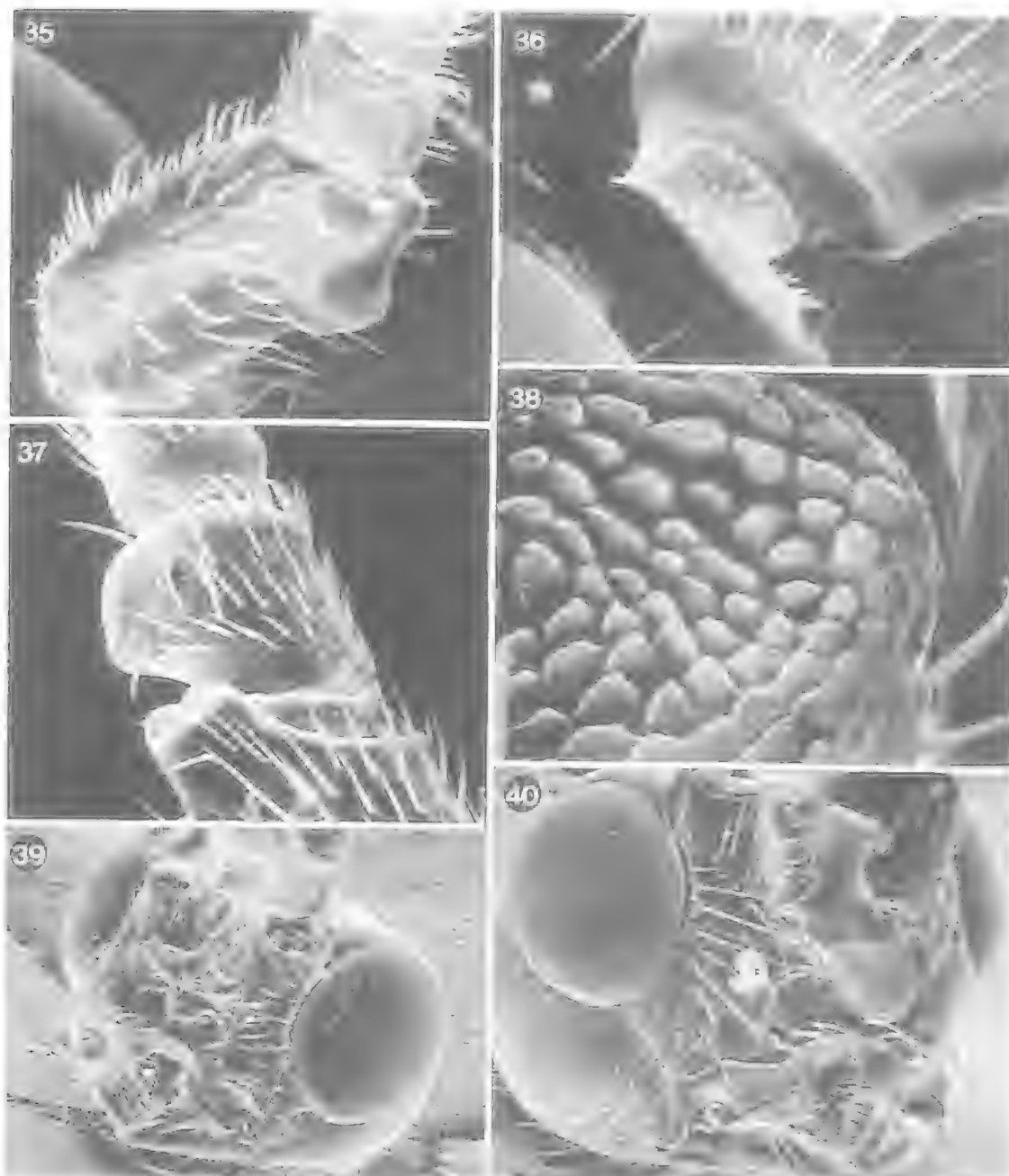
Lengths of fore femur: tibia : tarsus = 1.0:1.29:1.52. Lengths of hind femur: tibia: basitarsus = 1.3:2.4:1.0. Hind basitarsus 9 times longer than maximally deep.

Metasomal tergites largely evenly sculptured with fine, anastomosing, longitudinal ridges separated by rows of punctures (as in *huddlestoni* Quicke), but 5th tergite with longitudinal striation weaker and less regular. First tergite 1.1 times longer than posteriorly wide. Second tergite 1.5 times wider posteriorly than medially long. Posterior margin of 5th tergite with well-developed perimedial projections and with lateral emarginations.

Yellowish-brown except for antennae and apices of tarsi which are piceous and ovipositor sheaths which are black. Wings slightly hyaline with brown venation.

ETYMOLOGY

Named in honour of the senior author's father, Walter Jesse Quicke, for his years of patience.



FIGS 35–40. Features of scapus, pedicellus and face: 35, *Chaoilta* (*Chaoilta*) sp., scapus and pedicellus apico-medial aspect; 36, *Chaoilta* (*Chaoilta*) sp., base of scapus, lateral aspect; 37, *Chaoilta* (*Chaoilta*) sp., pedicellus, medial aspect; 38, *Chaoilta* (*Blastomorpha*) *decorata*, detail of apical part of pedicellus; 39, *Chaoilta* (*Chaoilta*) sp., head; 40, *Chaoilta* (*Blastomorpha*) *decorata*, head.

**Gelasinibracon* Quicke
(Figs 45, 71, 73, 10)

Small braconines of the tribe Braconini with

wing lengths less than 6mm. Known only from two closely related species: *G. sedlaceki* Quicke from Papua New Guinea and north Queensland and *G. simplicicaudatus* Quicke, only known

from Papua New Guinea (Quicke, 1989b). Nothing is known of their biology.

Habrobracon Ashmead
(Fig. 86)

Habrobracon is closely related to *Bracon*, which is probably paraphyletic because *Habrobracon* is classified separately. Cosmopolitan group of small wasps, with about twenty described species. Several species have been employed as biological control agents principally against stored product pests and *H. gelechiae* (Ashmead) has been introduced into Australia. *H. hebetor* (Say) is also recorded from Australia where it has been reared from *Cactoblastis cactorum*.

Hybogaster Szépligeti
(Figs 18, 30, 47, 67, 128)

Large wasps apparently related to the *Euurobraconini* (Quicke, 1988a). A principally Indo-Australian genus but with one species occurring in South Africa (Quicke, 1988a) and another in north Queensland. It should be noted however, that Parrott's (1953) record of *Hybogaster* from Australia is a misidentification of *Iphiaulax australiensis* Ashmead (Quicke, 1991a). Nothing is known of the biology of *Hybogaster* species but members of the related genus *Zeuzerilia* van Achterberg are parasites of Cossidae (van Achterberg, 1989).

Hyboteles van Achterberg
(Figs 72, 74, 105, 115)

Small wasps belonging to the subtribe *Aspidobraconina* of the *Braconini*. *Hyboteles* ranges from Brunei and the Philippines to north Australia and is monophyletic. Probably all *Aspidobraconina* are endoparasitoids of butterfly pupae; *Hyboteles toxopeusi* van Achterberg has been reared as a solitary endoparasitoid from a lycaenid pupa in Papua New Guinea (Quicke, 1987a, 1988b).

Iphiaulax Foerster
(Figs 32, 33, 63, 129)

Synonyms. *Anipphiaulax* Kokoujev; *Iphiaulacidea* Fahringer; *Euglyptobracon* Telenga

A large and virtually cosmopolitan genus of medium-sized braconines. Eight Australian species were treated by Quicke (1991a); several of

these had previously been wrongly placed in *Cynanopterus* Haliday or *Hybogaster* Szépligeti. Subsequently, the senior author has seen specimens of two undescribed Australian species in the collection of the AEIG. Nearly all members of the genus appear to be specialized parasitoids of cerambycid beetle larvae (Quicke, 1988b) but van Achterberg (1989) reported one species as having been reared from cossid moth larvae. Some species are frequently collected amongst mangroves and females are capable of giving a painful sting (DLJQ, pers. obs.).

Ligulibracon Quicke
(Figs 21, 42, 55, 88, 123)

A small genus of medium-sized to large *Aphrastobraconini* entirely restricted to Australia; apparently only the type-species, *L. levor* Quicke, is described though several others have been seen in collections by the senior author. Nothing is known of the biology of *Ligulibracon*, though, in common with other Australian *Aphrastobraconina*, they seem to be at least partially nocturnal (Quicke, 1992).

Macrobracon Szépligeti
(Figs 57, 58)

A small genus of large braconines belonging to the *Mesobracon* Szépligeti group (see Quicke, 1987b). *Macrobracon* ranges from north Queensland to south India; only one species, *M. nobilis* Turner, occurs in Australia (Shenefelt, 1978). Nothing is known of the biology of *Macrobracon* though members of the related oriental genus *Pseudoshirakia* van Achterberg attack stem-boring pyralid moth larvae in grain crops (Achterberg, 1983).

Megalommum Szépligeti
(Figs 22, 41, 49, 61)

Medium-sized species of *Aphrastobraconini* primarily from Australia, where there are many undescribed species, but also occurring in Papua New Guinea. Frequently collected at light (Quicke, 1992). The ovipositors of members of this genus collectively display a great deal of variation in length and shape but typically lack apico-ventral serrations probably indicating that oviposition takes place into a soft substrate.

Molibracon Quicke
(Figs 17, 133)

A monotypic genus of medium-sized wasps entirely restricted to Australia. *M. bimaris* (Turner) has been reared as a parasitoid of curculionid larvae, *Meriphus longirostris*, in *Banksia* cones (Quicke, 1988b). Most specimens seen by us are from Western Australia.

Myosoma Brullé
(Figs 2, 54, 70)

Synonyms. *Acanthobracon* Kriechbaumer; *Amyosoma* Viereck

A largely neotropical genus of small to medium-sized Braconini but with a few mostly smaller species known from the Old World tropics (Quicke & Wharton, 1989). *Myosoma rufescens* is the first true record of this genus in Australia (see Quicke, 1988b); *M. mutator* (Fabricius) belongs to *Pynobraconoides* gen. nov. *Myosoma* spp. appear to be principally parasitoids of concealed pyralid moth larvae (Shenefelt, 1978; Quicke & Wharton, 1989) but *M. chinensis* has also been reared from the larvae of the cossid *Zeuzera* in India, and *M. yanoi* (Watanabe) has been reared from larvae of the sesiid *Paranthrene regale* in Japan (Maetô, 1992).

Key to Indo-Australian species of *Myosoma*

1. Metasomal tergites 1-5 bright orange contrasting strongly with piceous or black tergites 6-9 (Fig. 2); head largely black *M. rufescens* sp. nov.
- Metasomal tergites unicolorous piceous or black; head variably coloured *M. chinensis* (Szépligeti) & other spp.

***Myosoma rufescens* sp. nov.**
(Fig. 2)

MATERIAL EXAMINED

HOLOTYPE: ♀ with the following labels: 'AUSTRALIA: ACT Canberra, Black Mtn. Jan 25-30. 1984 L. Masner, MT' & 'Dry sclerophyl Eucalyptus for.' From AEIG but on permanent loan to ANIC by agreement with collections manager.

PARATYPE: ♂ with following labels: 'QUEENSLAND: Mirani 34km NW Mackay X-16-79' and 'HE & MA Evans & A. Hook Coll.', ANIC.

DESCRIPTION (♀)

Length of body 5.7mm, of fore wing 5.5mm

and of ovipositor (part exerted beyond apex of metasoma) 1.3mm.

First flagellomere 1.07 times longer than both the 2nd and 3rd separately. Third flagellomere 1.4 times longer than wide. Height of clypeus: intertentorial distance: tentorio-ocular distance = 1.0: 3.7: 2.3. Face smooth medially; coriaceous and densely setose laterally. Height of eye: shortest distance between eyes: width of head = 1.05:1.0:2.0. Frons densely setose except along the median line. Post-ocellar line: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.4:1.0:3.57. Occiput largely glabrous. Horizontal length of eye 1.7 times horizontal length of head behind eye.

Mesosoma 1.5 times longer than high. Notauli weak but impressed along whole length of mesoscutum. Lateral lobes of mesoscutum glabrous.

Forewing. Lengths of veins SR1:3-SR: r = 3.9: 3.0: 1.0. Lengths of veins 2-SR:3-SR:r-m = 1.1: 2.0: 1.0. Pterostigma 3.15 times longer than maximally wide. Vein cu-a virtually interstitial. Vein 1-SR+M straight.

Hindwing. Lengths of veins 1r-m: SC+R1 = 1.0:1.7. Apex of vein C+SC+R with one especially thickened bristle. Base of wing evenly setose.

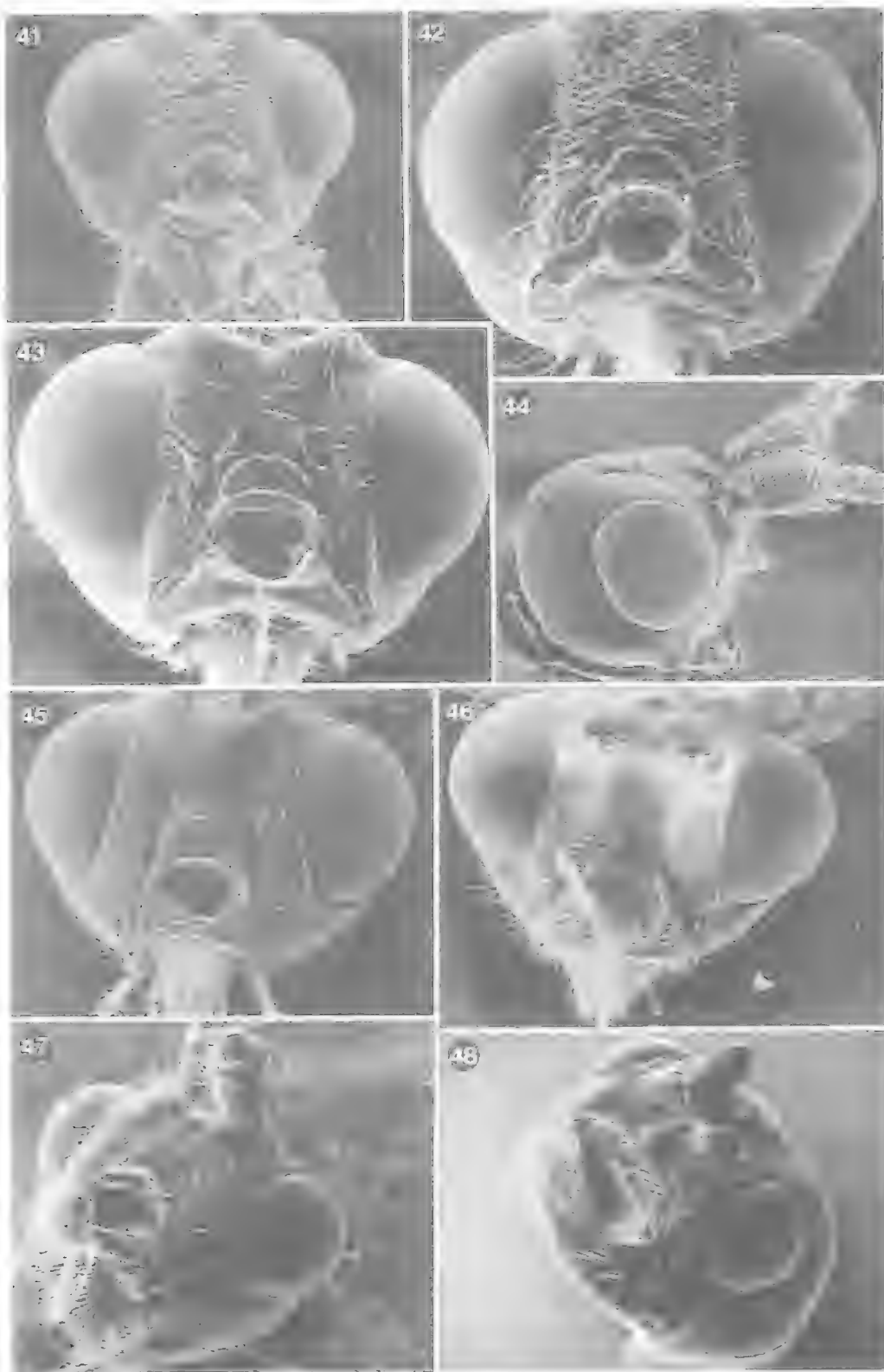
Lengths of fore femur: tibia: tarsus = 1.0: 1.1: 1.3. Lengths of hind femur: tibia: basitarsus = 1.9: 2.8: 1.0. Hind femur 3.2 times longer than maximally wide. Hind tarsus 7.0 times longer than maximally wide. Hind basitarsus 6.5 times longer than apically deep.

Metasoma smooth and shiny. First tergite approximately 2.2 times longer than maximally wide; lateral areas narrow but complete. Second tergite with antero-lateral corners with reduced sclerotization. Second suture straight, narrow, quite deep. Tergites 3 to 6 with irregular, sparse, short setosity posteriorly.

Pale orange brown to brownish yellow except for the following which are black or piceous: antennae; head except labio-maxillary complex, palps and base of mandibles; mid- and posterior legs; metasomal tergites 6 and 7; ovipositor sheaths. Wing membrane pale brown slightly paler distally; venation and pterostigma dark brown.

DESCRIPTION (♂)

As for female except slightly smaller and the middle leg is brownish yellow except for the telotarsus which is piceous.



***Paranesaulax Quicke**
(Figs 24, 99, 106, 127)

Medium-sized braconines known from only one described species from Papua New Guinea, *P. nitor* Quicke. A possibly conspecific individual from north Queensland has been seen by the authors. Nothing is known of the biology of this genus.

Pedinopleura van Achterberg
(Figs 78, 114, 121, 122)

Small species belonging to the Aspidobraconina. In addition to *P. australiensis* sp.nov., two non-Australian species have been described (Achterberg, 1984) but many undescribed ones occur in South Africa, India through Malaysia to New Guinea and north Australia. There are no host records for this genus but three other genera of the Aspidobraconina (*Aspidobracon* van Achterberg, *Hyboteles* van Achterberg and *Philomacroploea* Cameron) have been reared from butterfly pupae (van Achterberg, 1984; Quicke, 1987a).

Key to the Indo-Australian species of
Pedinopleura (♀♀ only)

1. Face, frons, temples and vertex smooth; lateral margin of syntergite 1+2+3 with an obvious notch (Fig. 122); antenna largely brownish becoming piceous apically ... *P. emarginata* van Achterberg
- Face, frons, temples and vertex striate (Fig. 78); lateral margin of syntergite 1+2+3 without notch, evenly curved or with a single posterior lobe (Fig. 121); antenna black 2
2. Metasomal tergites 3-5 with a dark spot on either side; posterior margin of 6th metasomal tergite with a well-developed emargination; lateral margin of syntergite without a posterior lobe; frons and vertex coarsely transversely striate *P. kosshuensis* (Watanabe)
- Metasomal tergites 3-5 unicolorous brownish yellow; posterior margin of 6th metasomal tergite only very weakly emarginate (Fig. 114); lateral margin of syntergite with a well-developed posterior lobe (Fig. 121); frons and vertex very finely transversely striate (Fig. 78) *P. australiensis* sp.nov.

Pedinopleura australiensis sp.nov.
(Figs 78, 114, 121)

MATERIAL EXAMINED

HOLOTYPE: ♀ with following labels: 'Ayr Queensland 4 Sep. 1950 E.F.Riek'. Deposited in ANIC.

PARATYPE: ♂ with same data as holotype. ANIC.

DESCRIPTION (♀)

Length of body 4.5mm, and of forewing 4.3mm, of ovipositor (part exerted beyond apex of metasoma) 1.1mm and of antenna 4.1mm.

Antenna with 36 flagellomeres. Terminal flagellomere pointed but not acuminate, 2.1 times longer than basally wide. Median flagellomeres approximately as wide as long. First flagellomere 1.3 times longer than both the 2nd and 3rd separately, the latter being 1.2 time longer than wide. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1:2:2. Height of eye: width of face: width of head = 1.0:1.5:1.77. Malar suture deep and narrow. Face with multiple, strong, parallel, transverse ridges. Eyes virtually glabrous. Frons and occiput finely subtransversely carinate. Head very transverse; horizontal length of head behind eye: horizontal length of eye = 2.35:1.0 Post-ocellar length: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.0:1.0:2.75.

Mesosoma 1.4 times longer than high; strongly sculptured, mostly punctate. Median area of metanotum with a complete mid-longitudinal carina. Precoxal suture not impressed; indicated by a band of punctures. Propodeum with a complete mid-longitudinal carina bordered by short, rather weak crenulations.

Forewing. Lengths of veins SR1:3-SR:r = 7.3:2.8:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.1:1.7:1.0 Vein 2-SR+M long, shortest distance between 1st discal cell and 2nd submarginal cell: length of vein m-cu = 1.7:1.0. Vein cu-a interstitial.

Length of fore femur: tibia: tarsus = 1.0:1.0:1.15. Length of hind femur: tibia: basitarsus = 1.94: 2.65: 1.0. Hind basitarsus 4.9 times longer than deep.

Metasoma with strong rugose sculpture. First tergite with a distinct median groove posteriorly. Posterior margin of 6th tergite very weakly emarginate. Ovipositor (part exerted beyond apex of metasoma) approximately 0.4 times length of forewing.

FIGS 41-48. Features of head: 41, *Megalommum* sp.; 42, *Ligulibracon* sp.; 43, *Eucurriea* sp.; 44, *Chaoilta* (*Chaoilta*) sp.; 45, *Gelasinibracon* sp.; 46, *Pycnobraconoides mutator* (Fabricius); 47, *Hybogaster* sp.; 48, *Euurobracon latitempus* Quicke.

Entirely honey-yellow except for antennae, hind tarsi, and ovipositor sheaths which are black or piceous. Wing membrane pale yellow tending to hyaline distally; vein C+SC+R and pterostigma piceous, remainder of venation yellowish.

DESCRIPTION (♂)

Very similar to female except smaller and posterior margin of 6th metasomal tergite only marginally emarginate and antenna dark rufous.

Ploceibracon Quicke (Figs 75, 79, 100)

Known only from the type species, *P. monstrans* Quicke, from New South Wales. The holotype of *P. monstrans* has a small dark mark indicating a trace of hindwing vein 3-CU and, together with the strong spur from fore-wing vein 3-CU1, this may indicate a relationship with *Calcaribracon*. Nothing is known of its biology.

Psittacibracon Quicke (Figs 9, 10, 132)

A rare monotypic genus of medium-sized Braconini entirely restricted to Australia. *Psittacibracon lacteolus* Quicke (Figs 9, 10) is known from a few specimens from South Australia, Western Australia and New South Wales. Nothing is known of its biology.

Pycnobraconoides gen. nov. (Figs 6, 46, 130)

TYPE SPECIES

Ichneumon mutator Fabricius 1775: 335.

DIAGNOSIS

Pycnobraconoides can be distinguished from other members of the tribe Braconini (sensu van Achterberg, 1983) by the following combination of characters: (i) head very transverse; (ii) eyes usually moderately to very setose; (iii) precoxal suture absent; (iv) hindwing vein 1r-m much shorter than vein SC+R1 (v) 2nd submarginal cell of forewing long; (vi) claws with rounded basal lobes; (vii) propodeum simple, without a mid-longitudinal carina; (viii) metasoma robust, 3rd tergite more than 2 times wider than long; (ix) ovipositor robust, without a pre-apical dorsal nodus but distinctly pre-apically expanded (Fig. 130); (x) mandibles (except for apex) white.

GENERIC DESCRIPTION

Antennae shorter than forewing, with approximately 40 flagellomeres. Terminal flagellomere acuminate. Median flagellomeres marginally longer than wide. Scapus small, shorter ventrally than dorsally in lateral aspect; not apico-medially emarginate. Labio-maxillary complex short. Mandibles ivory-white except for darker apex. Clypeus angled into hypoclypeus but without a transverse median carina: separated from face dorsally by a groove. Face smooth and shiny, setose. Eyes usually moderately to very densely setose; distinctly emarginate. Frons weakly impressed, largely setose, with a well-developed mid-longitudinal sulcus. Head very transverse; horizontal length of eye approximately 2.5 times longer than horizontal length of head behind eye.

Mesosoma smooth and shiny approximately 1.3 times longer than high. Mesosotum largely glabrous except for along line of notauli. Notauli weakly impressed anteriorly, not impressed posteriorly. Scutellar sulcus narrow, crenulate. Precoxal suture absent. Mesopleural suture smooth. Median area of metanotum not carinate. Propodeum without carinae. Propodeal spiracle small, round, situated near middle of propodeum.

Forewing. Vein 1-SR+M more or less straight. Vein 2-SR+M short, more or less interstitial. Second submarginal cell long, vein 3-SR approximately 0.8 times length of vein SR1. Veins C+SC+R and 1-SR forming an angle of approximately 75°. Vein r-m unsclerotized. Vein cu-a interstitial.

Hindwing. Vein 1r-m much shorter than vein SC+R1. Apex of vein C+SC+R with only one especially thickened bristle. Base of wing evenly setose.

Claws with rounded basal lobes. Hind tibia slender, with indistinct longitudinal, lateral groove.

Metasoma short, wide, robust, largely with rugose to strong punctate sculpture but largely smooth in some species. First tergite with dorso-lateral carinae; raised median area sculptured posteriorly, strongly sloping, smooth anteriorly. Second tergite wide, with or without elongate median area (defined largely by difference in sculpture); anterolaterally with a pair of longitudinal, sub-parallel grooves. Tergites 3 to 5 with posterior margins rounded in profile, rarely 5th with a weak transverse, subposterior groove. Ovipositor robust, pre-apically smoothly expanded pre-apically (Fig. 130), ventral valves without or with extremely reduced serrations; part exerted



FIGS 49-58. 49-51, apex of hindwing vein C+SC+R showing specialised bristles: 49, *Megalomum*.; 50, *Callibracon* sp.; 51, *Bracon* sp. 52-58, features of claws: 52, *Calcaribracon willani* sp.nov.; 53, *Bracon* sp.; 54, *Mysosoma* sp.; 55, *Ligulibracon* sp.; 56, *Euurobracon* sp.; 57-58, *Macrobracon* sp.

beyond apex of metasoma slightly shorter than medial length of metasomal tergite 2+3.

MALES

Very similar to females. Intertergal metasomal glands well-developed with a pair of large sac-like reservoirs (Quicke, 1990). Genitalia: digitus with a single apical tooth; parameres with only a single row of setae apically.

BIOLOGY

From many, largely unpublished, records it is clear that *Pycnobraconoides* gen.nov. is a specialised parasitoid of cryptocephaline chrysomelid beetle larvae (Quicke, 1988b). The beetle larvae (and pupae) live in a case from which single specimens of *Pycnobraconoides* commonly emerge. The following cryptocephalines have been recorded as hosts of various species of *Pycnobraconoides*: '*Cadmus*' *aurantiacus*, *Cryptocephalus speciosus*, *Lachnabothra* sp., and *Prasonotus* sp. It is presumed but not proven that *Pycnobraconoides* is ectoparasitic.

DISCUSSION

Pycnobraconoides gen.nov. appears to be most closely related to the oriental genus *Pycnobracon* Cameron which was originally described from India (Cameron, 1902), and recently members of the new genus have been dealt with under *Pycnobracon*. However, it has been recognised for some time that the Australian representatives do not fit well in *Pycnobracon*. Indeed, Quicke (1987b) considered *Pycnobracon* to comprise two sections; those keying out at couplet 108 (loc. cit.), which are referable to *Pycnobracon* sensu stricto; and those keying out at couplets 90 and 94, which are placed here under *Pycnobraconoides* gen.nov. In particular, *Pycnobraconoides* differs from *Pycnobracon* in having a robust ovipositor without a pre-apical dorsal nodus and an extremely transverse head. The biologies of the two genera also differ considerably with *Pycnobracon* sensu stricto parasitic on pyralid moth larvae while *Pycnobraconoides* attacks case-bearing Chrysomelidae (see above). Within Australia, the new genus is widely distributed and specimens representing a small number of species have been seen from Australian Capital Territory, Queensland, New South Wales, Tasmania and Western Australia.

INCLUDED SPECIES

Pycnobraconoides froggattii (Cameron) comb.nov.

(= *Bracon froggattii* Cameron, 1911: 339); holotype in BMNH examined.

Pycnobraconoides mutator (Fabricius) comb. nov. (= *Iphiaulax bipartitus* Szépligeti 1905:35; junior subjective synonym, Quicke, 1991c).

**Rostraulax* Quicke (Fig. 104)

Rostraulax species are medium-sized wasps found primarily in Indonesia and New Guinea. One species, *R. xanthocephalus* (Turner), is found in Queensland and northern New South Wales rainforests as well as in Papua New Guinea. Nothing is known of the biology of *Rostraulax* but the apparently related genus *Cratobracon* has been reared from wood-boring cerambycid larvae (Quicke, unpubl. obs.). *Rostraulax* is very closely related to *Shelfordia* Cameron and may need to be synonymized with that genus (van Achterberg, pers. comm.).

Serratobracon Tobias (Figs 83, 85, 107)

This genus is known from only a single specimen from the Northern Territory which has a highly characteristic combination of pedicellus and scapus morphology. Its affinities were discussed by Tobias in Quicke & Tobias (1990), who concluded that it may be related to either *Sylviobracon* Quicke or to the *Atamychus* group of genera (Quicke, 1987b). However, neither of these placements is satisfactory and more material needs to be studied.

Simplicibracon Quicke (Figs 5, 76, 102)

Previously, species of this genus were only known from Taiwan (Quicke, 1988e) and Japan (Maetô, 1991). In addition to these and the new Australian species, the senior author has seen specimens of another new species from Fiji. In *Simplicibracon*, the strongly developed transverse median clypeal carina (Fig. 76) is quite distinctive and most species (except for two seen from Japan) have hind wing vein 2-SC+R slightly transverse. The one species for which the biology is known, *S. curticaudis* Maetô, is a parasitoid of leaf-galling Cecidomyiidae on broad-leaved, evergreen trees (Maetô, 1991).

Key to the species of *Simplicibracon* (♀♀ only)

1. Hindwing vein 2-SC+R longitudinal (see Fig. 101); ovipositor (part exerted beyond apex of metasoma) less than 0.25 times length of forewing; metasomal tergites unicolorous brownish yellow to yellowish brown; 2nd metasomal tergite less than 1.8 times wider than medially long *S. curticaudis* Maciô
- Hindwing vein 2-SC+R transverse (Fig. 102); ovipositor (part exerted beyond apex of metasoma) more than 0.35 times length of forewing; metasomal tergites brownish yellow to whitish yellow, marked with brown or black blotches on tergites 2 and 3 or 3 and 4; 2nd metasomal tergite more than 1.8 times wider than medially long 2
2. Notauli crenulate; metasomal tergites metasomal tergites 5-7 yellow-brown, same as tergites 1 and 2 *S. maculigaster* Quicke
- Notauli smooth; metasomal tergites 5-7 cream-white, different from tergites 1 and 2 *S. nigratarsus* sp. nov.

***Simplicibracon nigratarsus* sp. nov.**
(Figs 5, 76, 102)

MATERIAL EXAMINED

HOLOTYPE: ♀ with the following labels: '15.41S 145.12E Annan Riv. 3Km WbyS Black Mt. 26-27 Apr. 1981Q, I.D. Naumann ex ethanol' & 'collected at light'. Deposited in ANIC.

DESCRIPTION (♀)

Length of body 4.2mm, of fore wing 4.6mm, of ovipositor (part exerted beyond apex of metasoma) 1.9mm, and of antenna 4.1mm.

Antennae with 32 flagellomeres. First flagellomere 1.3 times longer than both the 2nd and 3rd separately, the latter being 1.5 times longer than wide. Transverse median clypeal carina strongly protruding. Height of clypeus (upper part): intertentorial distance: tentorio-ocular distance = 1.0:1.82:1.63. Face shiny with moderately well-developed punctures at the bases of the setae. Height of eye (measured parallel to face): width of face: width of head = 1.0:1.18:2.36. Face 2 times wider than high. Eyes weakly setose. Frons without a mid-longitudinal ridge; weakly impressed. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.43:1.0:3.14.

Mesosoma 1.24 times longer than high. Pronotum largely smooth and shiny with narrow crenulate groove laterally. Mesonotum moderately

setose posteriorly and laterally but anterior third of middle lobe virtually glabrous. Notauli moderately impressed, not crenulate. Precoxal suture represented by only a weak rounded depression.

Forewing. Lengths of veins SR1:3-SR:r = 5.6:1.9:1.0. Lengths of veins 2-SR: 3-SR: r-m = 1.6:1.9:1.0. Vein r-m with only a single posterior bulla and associated flexion line. Length of vein m-cu: shortest distance between 1st subdiscal cell and 2nd submarginal cell = 0.8:1.0.

Hindwing. Base of wing more or less evenly, densely setose. Vein 2-SC+R distinctly transverse. Apex of vein C+SC+R with only one especially thickened bristle.

Lengths of fore femur: tibia: tarsus = 1.0:1.13:1.3. Fore tibia moderately densely with strong spine-like setae antero-laterally. Lengths of hind femur: tibia: basitarsus = 1.8:2.55:1.0. Hind tibia very robust, 6.1 times longer than maximally deep. Hind basitarsus 4.4 times longer than deep.

Metasoma with rugulose sculpture. Second tergite 2.1 times wider than medially long. Ovipositor (part exerted beyond apex of metasoma) approximately 0.4 times length of forewing.

Brownish yellow except for the following: antennae, hind tibia except extreme base, hind basitarsus, a pair of large submedial marks on the 3rd and 4th tergites, ovipositor sheaths, black. Lateral parts of 3rd and 4th tergites and all except for a mid-longitudinal yellow line on tergites 5 to 7, white. Wings pale smoky brown with brown venation.

NOTE

The holotype of *S. nigratarsus* sp. nov. is the same specimen as referred to by Quicke (1992).

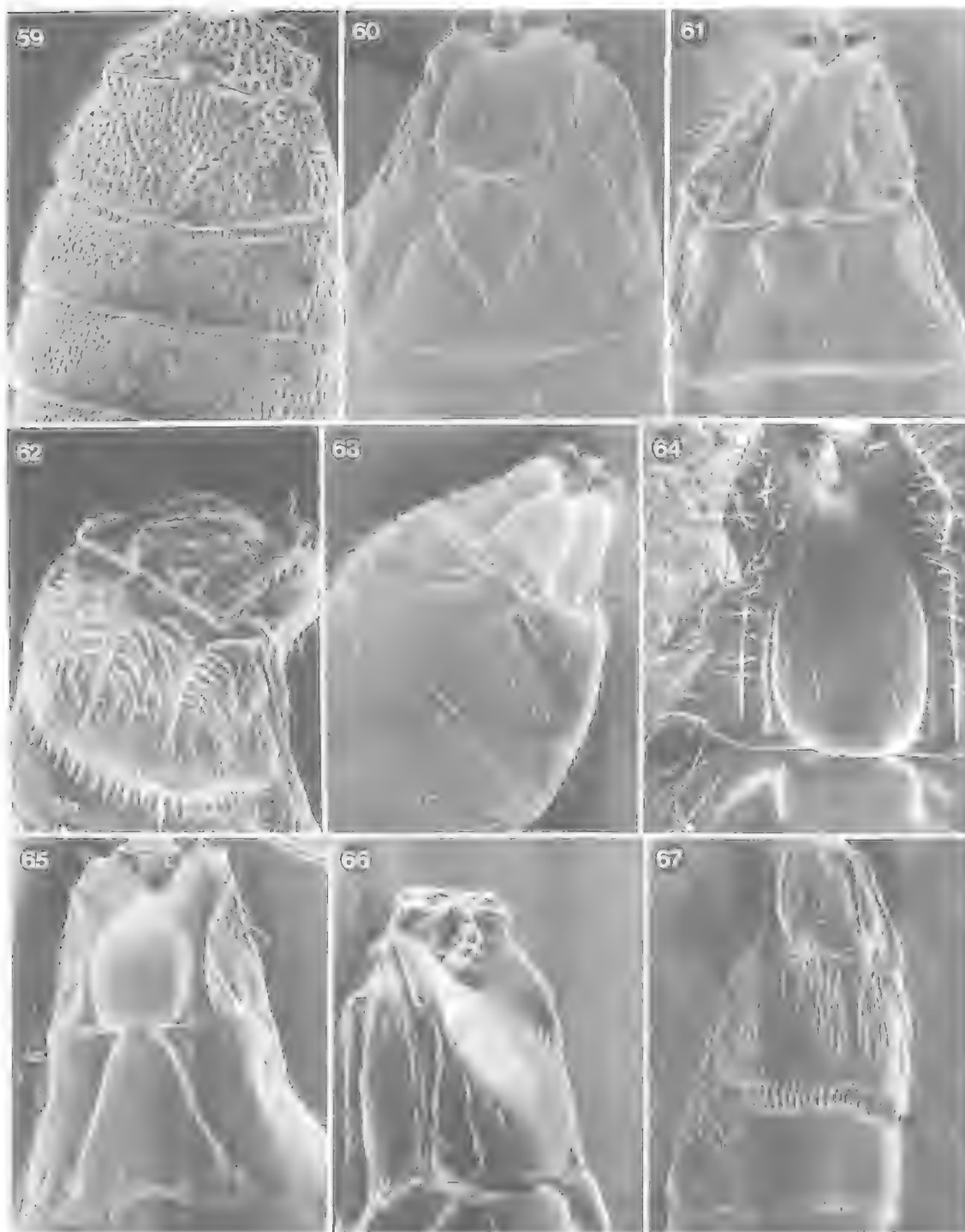
***Stenobracon* Szépligeti**
(Fig. 93)

Synonyms. *Elphea* Cameron; *Phanuulux* Cameron

A small genus of medium-sized wasps belonging to the tribe Bathyaulacini. One probably undescribed species is found in the north of Western Australia in the Kimberleys. Elsewhere, *Stenobracon* spp. are important parasitoids of Lepidoptera larvae that bore in stems of grain crops (Quicke, 1983; 1988c) but nothing is known about the biology of the Australian species.

***Stigmatobracon* Turner**
(Figs 1, 131)

A small genus of medium-sized to large wasps.



FIGS 59-67. Features of the metasoma: 59, *Tropobracon* sp. (African) T1-T4; 60, *Eutesaulus* sp., T1-T2; 61, *Megalommum* sp., T1-T2; 62, *Campyloneurus* sp., Tj1-T2; 63, *Iphiaulax* sp., T1-T3; 64, *Callibracon* sp., T1; 65, *Virgulibracon* sp., T1-T2; 66, *Vomeribracon* sp., T1; 67, *Hybogaster* sp., T1-T4.

A key to the four described species, all from Australia, is provided by Turner (1918). However, the senior author has seen a female of *S. xanthostigma* Turner from Papua New Guinea and also males with somewhat different colouration also from Papua New Guinea. These may represent a new species, though the possibility of sexual dimorphism in this group cannot be ruled out. Nothing is known of their biology though one species has been collected amongst mangroves (*Rhizophora*) in north Queensland, and other specimens have been collected in the Northern Territory, Victoria and Western Australia.

Testudobracon Quicke
(Figs 116-120)

Small wasps belonging to the Braconini. Only a few species have been described but we are aware of many undescribed ones from both Africa and the Indo-Australian region. *Testudobracon* species are apparently specialist ectoparasitoids of gall-forming, cecidomyiid Diptera, especially — and perhaps exclusively — Asphondyliini (Quicke 1986a; Maetô, 1991). This is also partly confirmed by an Australian host record for the genus, based on an apparently undescribed species represented in the QDPI collection, which had been reared from a gall on '*A. polycarpa*'.

Key to the species of *Testudobracon* (♀♀ only)

1. Median emargination of 6th metasomal tergite shallow and with rounded lateral margins (Fig. 120); ovipositor (exserted part) at least 0.75 times length of forewing; precoxal suture (if distinguishable), represented by a weak, complete, narrow, longitudinal groove 2
- Median emargination of 6th metasomal tergite deep and with sharply defined (angular) lateral margins (Figs 117, 118); ovipositor (exserted part) less than 0.75 times length of forewing; precoxal suture present as a deep, smooth, rounded pit 3
2. Hind leg almost entirely pale yellow-brown; metasomal tergites 4-6 largely whitish, except for basal (anterior) third which is yellowish and postero-lateral lobes which are somewhat darker; vertex with distinct fine transverse, striate sculpture; metasomal tergites 4-6 rugulose *T. longicaudis* Maetô
- Hind leg almost entirely black; metasomal tergites 4-6 with basal (anterior) half black or piceous brown, and posterior half white; vertex totally smooth and shiny; metasomal tergites 4-6 irregu-

larly punctate (Fig. 120) *T. australicollis* sp. nov.

3. Postero-lateral margin of 6th metasomal tergite with a pointed protuberance (Fig. 116) 4

- Postero-lateral margin of 6th metasomal tergite with a rounded lobe-like protuberance (Fig. 119) 5

4. Middle lobe of mesoscutum largely glabrous except for line of notauli; body and legs virtually entirely brownish yellow *T. unicoloris* sp. nov.

- Middle lobe of mesoscutum largely setose (except for anterior face); body and legs commonly with black or piceous markings especially frons, vertex, part of mesopleuron, metanotum and propodeum, middle coxae and hind coxa and hind femur *T. pleuralis* (Ashmead)

5. Body and legs (except telotarsi) entirely pale brownish yellow; postero-lateral margin of 6th metasomal tergite hardly produced *T. taryanae* sp. nov.

- Body and hind legs extensively marked with black and dark reddish-brown, metasoma with obvious pattern of dark red, black and white *T. niger* Quicke

Testudobracon australicollis sp. nov.
(Fig. 120)

MATERIAL EXAMINED

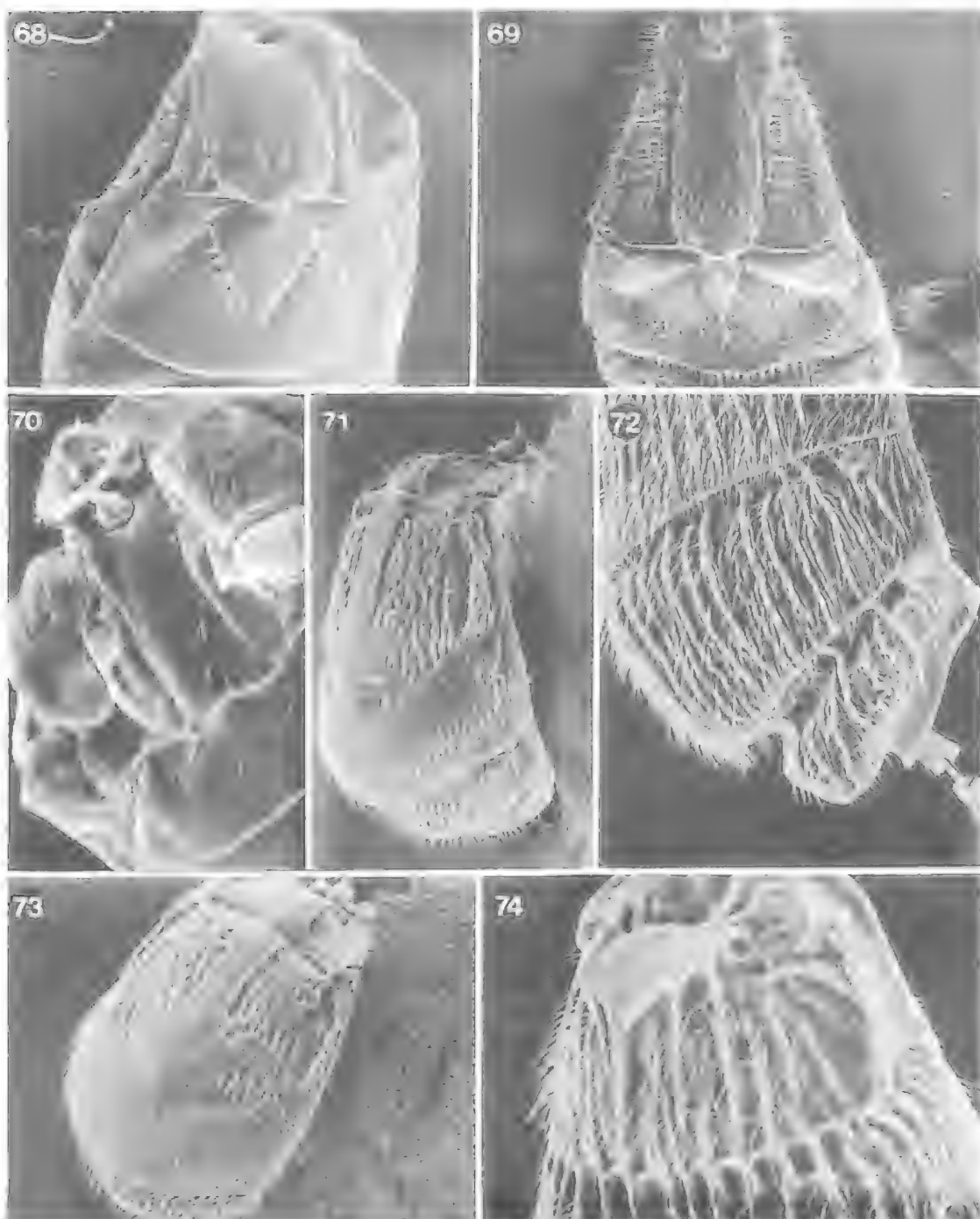
HOLOTYPE: ♀ with following labels: 'Mackay Queensland 1909-45', '834' & 'Mackay 3.92'. In collection of BMNH.

DESCRIPTION (♀)

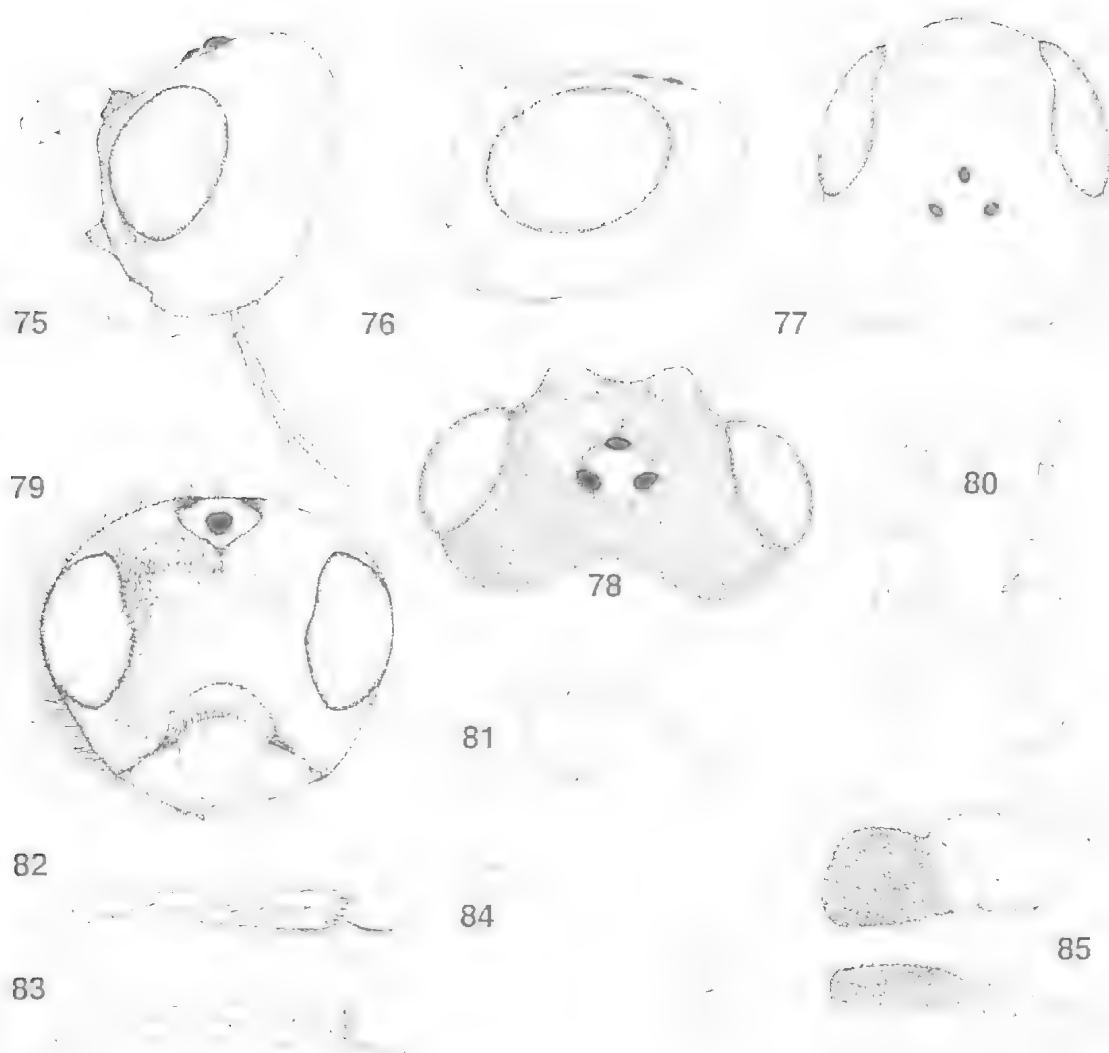
Length of body 3.7 mm, of forewing 3.6 mm and of ovipositor (part exserted beyond apex of metasoma) 2.9 mm.

First flagellomere 1.1 times longer than both the 2nd and 3rd separately, the latter being 1.8 times longer than wide. Height of clypeus: intertentorial distance: tentorio-ocular distance = 1.0:2.2:1.58. Malar space 0.23 times height of eye. Face smooth and shiny medially, finely coriaceous laterally, without an obvious mid-longitudinal ridge. Height of eye: width of face: width of head = 1.0:1.1:2.1. Eyes sparsely short setose. Frons finely coriaceous medially, smooth and shiny laterally. Shortest distance between posterior ocelli: transverse diameter posterior ocellus: shortest distance between posterior ocellus and eye = 1.65: 1.0: 3.5. Horizontal length of eye 2.6 times horizontal length of head behind eye.

Mesoscutum smooth and shiny, setosity largely restricted to line of notauli. Precoxal suture rep-



FIGS 68-74. Features of the metasoma: 68, *Eumesaulax* sp., T1-T2; 69, *Chaoilta* (*Blastomorpha*) *decorata* Szépligeti, T1-T2; 70, *Myosoma* sp. (Indo-Australian), T1; 71, *Gelasinibracon* sp., T1-T5; 72, *Hyboteles* sp., T5-T6; 73, *Gelasinibracon* sp., T1-T3; 74, *Hyboteles* sp., T1.



FIGS 75-85. Features of head, mesosoma and legs: 75, *Ploceibracon monstans* Quicke; 76, *Simplicibracon nigratarsus* sp.nov.; 77, *Atanycolus australiensis* sp.nov.; 78, *Pedinopleura australiensis* sp.nov.; 79, *Ploceibracon monstans* Quicke; 80, *Atanycolus australiensis* sp.nov., base of antenna, dorso-lateral and dorsal aspects; 81, *Furcadesha walteri* sp.nov., scapus, lateral aspect; 82, *Atanycolus australiensis* sp.nov., fore tibia; 83, *Serratobracon cardaleae* Tobias, fore tibia; 84, *Atanycolus australiensis* sp.nov., profile mesoscutum and pronotum; 85, *Serratobracon cardaleae*, scapus and pedicellus, lateral and dorsal aspects.

resented by a complete but very weak, smooth, longitudinal groove.

Length of forewing veins SR1:3-SR:r = 5.2:2.8:1.0. Lengths of veins 2-SR:3-SR:r-m = 2.1:3.1:1.0.

Lengths of fore femur: tibia: tarsus = 1.05:1.0:1.2. Lengths of hind femur: tibia: basitarsus = 2.5:3.1:1.0. Hind tibia 5.7 times longer than wide.

Second metasomal tergite 2.7 times wider than medially long, with weak parallel-sided, smooth narrow median area, and with posteriorly converging, antero-lateral, longitudinal grooves nearly reaching posterior margin. Third tergite 2.9 times wider than medially long. Tergites 3 to 6 with weakly-developed, rounded postero-lateral lobes. Sixth tergite weakly emarginate me-

dially. Ovipositor approximately 0.8 times length of forewing.

Head, mesosoma fore and mid legs pale brownish orange except for piceous mark on top of head. Median parts of metasomal tergites 1-3 broadly brown to piceous, laterally whitish. Tergites 4-6 basally piceous brown, posteriorly white. Hind legs black. Wings pale brown with light to dark brown venation.

***Testudobracon unicolorus* sp.nov.**
(Figs 116, 117)

MATERIAL EXAMINED

HOLOTYPE: ♀ with following labels: 'S.E. Queensland, Tamborine Mts. 19-26. iv. 1935' and 'AUSTRALIA: R.E. Turner B.M. 1935-240'. In BMNH collection.

DESCRIPTION (♀)

Length of body 2.6mm, of forewing 2.9mm and of ovipositor (part exerted beyond apex of metasoma) 1.7mm.

First flagellomere 1.2 and 1.4 times longer than the 2nd and 3rd respectively, the latter being 1.7 times longer than wide. Height of clypeus: intertentorial distance: tentorio-ocular distance = 1.0: 2.3: 1.7. Face largely finely coriaceous. Height of eye: width of face: width of head = 1.0: 1.1: 2.05. Eyes glabrous, not emarginate. Top of head shiny. Shortest distance between posterior ocelli: transverse diameter posterior ocellus: shortest distance between posterior ocellus and eye = 1.2: 1.0: 2.9. Horizontal length of eye 2.5 times horizontal length of head behind eye.

Mesosoma approximately as long as high. Notauli weak but distinct along whole length. Mesosutum setose medio-posteriorly, along line of notauli and laterally. Precoxal suture represented by a deep pit.

Lengths of veins SR1:3-SR:r = 6.72: 2.5: 1.0. Lengths of veins 2-SR:3-SR:r-m = 1.25: 1.75: 1.0. Pterostigma 3.0 times longer than maximally wide.

Lengths of fore femur: tibia: tarsus = 1.0: 1.0: 1.27. Lengths of hind femur: hind tibia:

hind basitarsus = 2.3: 2.75: 1.0. Hind tibia 6 times longer than maximally deep. Hind basitarsus 4.4 times longer than deep.

Second metasomal tergite 2.47 times wider than medially long; more or less uniformly foveate rugose, without mid-basal area and with only weak sub-lateral grooves anteriorly. Third tergite 2.57 times wider than medially long. Tergites 3-5 with well-developed, rounded, postero-lateral lobes. Tergite 6 postero-laterally with a pointed prominence and medially deeply semicircularly incised.

Uniformly pale brownish yellow except antennae and ovipositor sheaths which are black. Wings very pale brown with dark brown venation.

***Testudobracon tatyanae* sp.nov.**
(Fig. 118)

MATERIAL EXAMINED

HOLOTYPE: ♀ with following labels: 'Mackay, Queensland, 1909-45.' and 'Mackay 1.01'. The type specimen is the right hand of two braconids glued to a single card square, in the BMNH collection.

DESCRIPTION (♀)

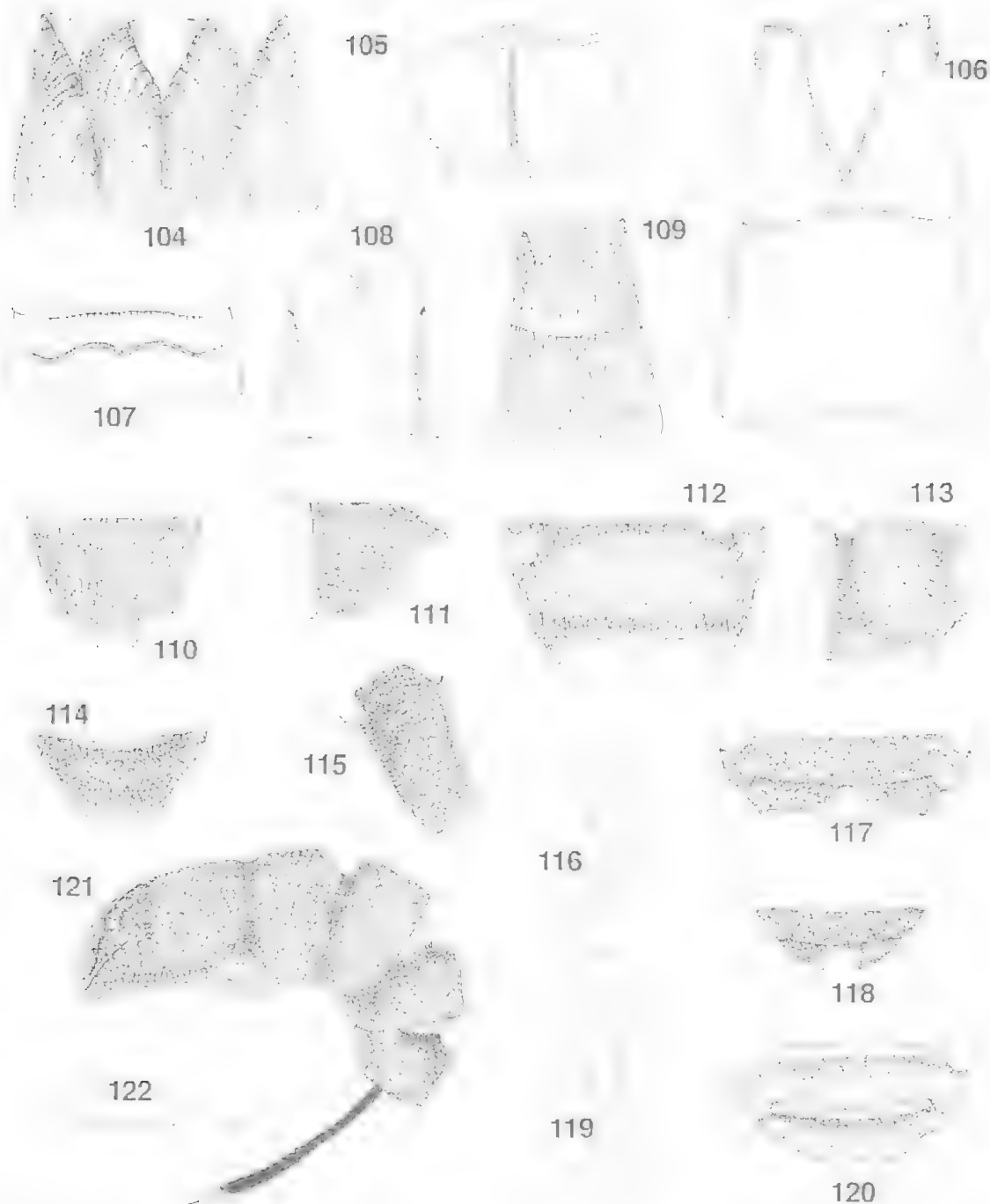
Length of body 2.25mm, of forewing 2.9mm, of ovipositor (part exerted beyond apex of metasoma) 1.6mm, and of antenna 2.6mm [face not visible, glued on to card].

Antennae with 23 flagellomeres. Terminal flagellomere 2 times longer than wide. First flagellomere 1.1 times longer than both the 2nd and 3rd separately, the latter being 1.7 times longer than wide. Head very transverse. Horizontal length of eye 2.3 times longer than horizontal length of head behind eye. Vertex and temples smooth and shiny.

Mesosoma 1.15 times longer than high. Mesosutum setose medio-posteriorly and along lines of notauli, otherwise smooth, shiny and glabrous. Precoxal suture represented by a smooth, deep, circular pit.

Lengths of forewing veins SR1:3-SR:r =

FIGS 86-103. Features of wing venation: 86, *Habrobracon* sp., pterostigma and 2nd submarginal cell; 87, *Trigastrotrothea tricolor* sp.nov. 88-89, 2nd submarginal cell; 88, *Ligulibracon levor* Quicke; 89, *Furcadesha wallert* sp.nov. 90-93, forewing vein 1-SR+M; 90, *Vomeribracon* sp.; 91, *Calcaribracon willani* sp.nov.; 92, *Virgulibracon endoxylaphagus* sp.nov.; 93, *Stenobracon* sp. 94-100, 1st subdiscal cell; 94, *Cedilla cedilla* Quicke; 95, *Calcaribracon willani* sp.nov.; 96, *Eutrobracon latitempus* Quicke; 97, *Eumesaulex terebrator* Tobias; 98, *Vipiellus* sp.; 99, *Paranesaulex* sp.nr. nitor; 100, *Placibracon monstrans* Quicke. 101-102, junction of hindwing veins 1r-m and SC+R1, to show orientation of 2-SC+R (between these): 101, *Gelasinibracon* sp.; 102, *Simplicibracon nigratarsus* sp.nov.; 103, *Atanycolus australiensis* sp.nov., apex of hindwing vein C+SC+R.



FIGS 104-122. Features of abdomen: 104, *Rostraulax xanthocephalus* (Turner), T2; 105, *Hyboteles toxopeusi* van Achterberg, propodeum; 106, *Paranesaulax* sp., T1-T2; 107, *Serratobracon cardaleae* Tobias, T3; 108 *Vomeribracon* sp., T1; 109, *Africadesha tobiasi* sp.nov., T2-T3; 110-111, *Furcadesha walteri* sp.nov., T5; 112-113, *Trigastrotheca tricolor* sp.nov., T5; 114, *Pedinopleura australiensis* sp.nov., T6; 115, *Hyboteles toxopeusi* van Achterberg, T6; 116, 117 *Testudobracon unicolorus* sp.nov., T5-T6; 118, *Testudobracon tatyanae* sp.nov., T5-T6; 119-120, *Testudobracon australicolorus* sp.nov., T5-T6; 121, *Pedinopleura australiensis* sp.nov.; 122, *Pedinopleura emarginata* van Achterberg, profile of lateral margin of syntergite T1-T3.

5.7:2.0:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.47:1.53:1.0.

Lengths of fore femur: tibia: tarsus = 1.0: 1.05: 1.5. Lengths of hind femur: tibia: basitarsus = 2.8: 3.1: 1.0. Hind tibia 5.8 times longer than maximally deep. Hind basitarsus 3.8 times longer than deep.

Metasoma more elongate than typical *Testudo-bracon*. Second tergite 2.1 times wider than medially long; without mid-basal area but with moderately-developed sub-lateral grooves. Third tergite 2.25 times wider than medially long. Tergites 3 to 5 with very weak, rounded postero-lateral lobes. Sixth tergite with a deep, semi-circular medial emargination.

Entirely pale brownish yellow except for antennae and ovipositor sheaths which are black and telotarsi which are slightly darkened. Wings weakly infuscate with brown venation.

ETYMOLOGY

Named after the senior author's wife Tanya for her tolerance of things hymenopterological.

**Trigastrotheca* Cameron
(Figs 3, 13, 87, 112, 113)

Synonyms. *Coelodontus* Roman; *Odontopygia* Enderlein.

This is a small but widely-distributed genus originally described from Africa (*T. trilobata* Cameron) but is also known from India, the Philippines (Quicke, 1987b) and now Australia. Nothing is known of the biology of this group of Braconini though members of the closely related genus *Kenema* van Achterberg have been collected on several occasions from fields of grain crops.

Key to non-African species of *Trigastrotheca* (♀ ♀ only)

1. Forewing vein 3-SR more than 1.4 times longer than vein r-m; mesosoma uniformly orange; 2nd metasomal tergite unicolorous, ivory white; 3rd to 5th metasomal tergites orange. *T. tricolor* sp. nov.
- Forewing vein 3-SR less than 1.25 times longer than vein r-m; mesosoma black, marked with ivory white; 2nd metasomal tergite black medially, white laterally; 3rd to 4th metasomal tergites largely black, 5th ivory white *T. tridentata* (Enderlein)

Trigastrotheca tricolor sp. nov. (Figs 3, 87, 112, 113)

MATERIAL EXAMINED

HOLOTYPE: ♀ with following labels: '7-14m. W. of Herberton, via Watsonville' and 'N. Queensland. 1 May 1967 D.H. Colless'. In ANIC collection.

PARATYPE: ♀ with same data as holotype. ANIC.

DESCRIPTION (♀ ♀)

Length of body 4.1 mm, of forewing 4.2 mm and of ovipositor (part exerted beyond apex of metasoma) 1.3 mm.

Antenna with 40 flagellomeres. Terminal flagellomere acuminate, 2.1 times longer than wide. Penultimate flagellomere 1.3 times longer than wide. Median flagellomeres 1.3 times longer than wide. First flagellomere as long as the 2nd and 3rd separately, the latter 1.7 times longer than wide. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0: 2.5: 2.0. Face finely punctate to coriaceous, otherwise shiny. Malar suture narrow but well-developed. Height of eye: width of face: width of head = 1.0: 1.2: 2.3. Frons flat without a mid-longitudinal ridge or lamella. Top of head finely coriaceous. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.3: 1.0: 2.5.

Mesosoma 1.46 times longer than high, largely with punctate sculpture on background of punctulate sculpture. Pronotum with finely crenulate groove. Notauli distinctly impressed along whole length of mesoscutum. Pre-scutellar sulcus narrow, with 6-7 crenulae. Scutellum rather flat, with reduced sculpture. Precoxal suture weak. Posterior margin of propodeum crenulate.

Forewing. Lengths of veins SR1:3-SR:r = 5.5:2.05:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.15:1.5:1.0. Vein r issuing approximately 0.4 distance from base pterostigma. Vein 2-SR+M long, 0.3 times length of 2-M. Vein cu-a interstitial, straight, perpendicular.

Hindwing. Apex of vein C+SC+R with one especially thickened bristle. Base of wing with a glabrous area.

Claws with rounded basal lobes. Length of fore femur: tibia: tarsus = 1.0: 1.1: 1.2. Length of hind femur: tibia: basitarsus = 2.2: 3.0: 1.0. Hind tibia moderately slender without an obvious longitudinal, lateral groove.

Metasomal tergites 1-5 foveate rugose. Tergite 1 with ill-defined dorsal carinae. Tergites 3-5 with well-developed antero-lateral areas. Ovipositor (part extending beyond apex of meta-

soma) approximately 0.3 times length of forewing.

Largely yellow-brown (ochreous) except for the following: antennae black; head piceous brown with palps, labio-maxillary complex, labrum, mandibles except apex and two large, sub-rectangular areas laterally on the frons to temple area, pinkish ivory; two lines along the notauli, the posterior half of the middle lobe of the mesoscutum and the scutellum paler ochreous than remainder of mesosoma; propleuron piceous brown; mid- and posterior legs piceous brown with the junction between femur and tibia, and the tarsi paler brown; first and second metasomal tergites, the antenno-lateral areas of the third tergite and a narrow posterior margin of the two semi-circular emarginations of the fifth tergite, ivory white; postero-lateral corners of fifth tergite piceous; ovipositor sheaths black. Wings pale brown, slightly darker apically; venation dark brown except extreme base of pterostigma which is whitish.

Tropobracon Cameron
(Figs 15, 59)

Synonym: *Shirakia* Viereck

Small species of Braconini distributed from Australia (Queensland) to India and Africa and also occurring in the Palaearctic Region (China). Elsewhere, *Tropobracon* species have frequently been reared from pyralid moth larvae boring in stems of grain crops including rice. The occurrence of the genus in Australia was noted by Quicke (1988b).

Undabracon Quicke
(Fig. 125)

A small genus of small to medium-sized Aphrastobraconini. Only two species have been described, *U. nigrithorax* Quicke from Australia and *U. sinuatus* (Baltazar) from the Philippines though we have seen two other undescribed species from Australia. Nothing is known of the biology of *Undabracon* though they are apparently nocturnal or crepuscular in habit (Quicke, 1992). Their arched ovipositor is reminiscent of that of another braconine genus, *Zaglyptogastra* Ashmead, which includes Afrotropical species

that attack twig-boring cerambycid beetle larvae, probably through frass holes (Quicke, 1991b). One Australian species has been observed flying near fallen wood.

Vipielus Roman
(Figs 25, 98)

The species of *Vipielus* are small to medium-sized braconines found only in Australia. *Vipielus* is closely related to the genera of Aphrastobraconini though it typically lacks the distinctive thickening of forewing vein CU1b. Species of *Vipielus* have been reared several times from stem-boring xyloxyctid larvae (Lepidoptera) including the macadamia twig-girdler, *Neodrepta luteotinctella* (Walker).

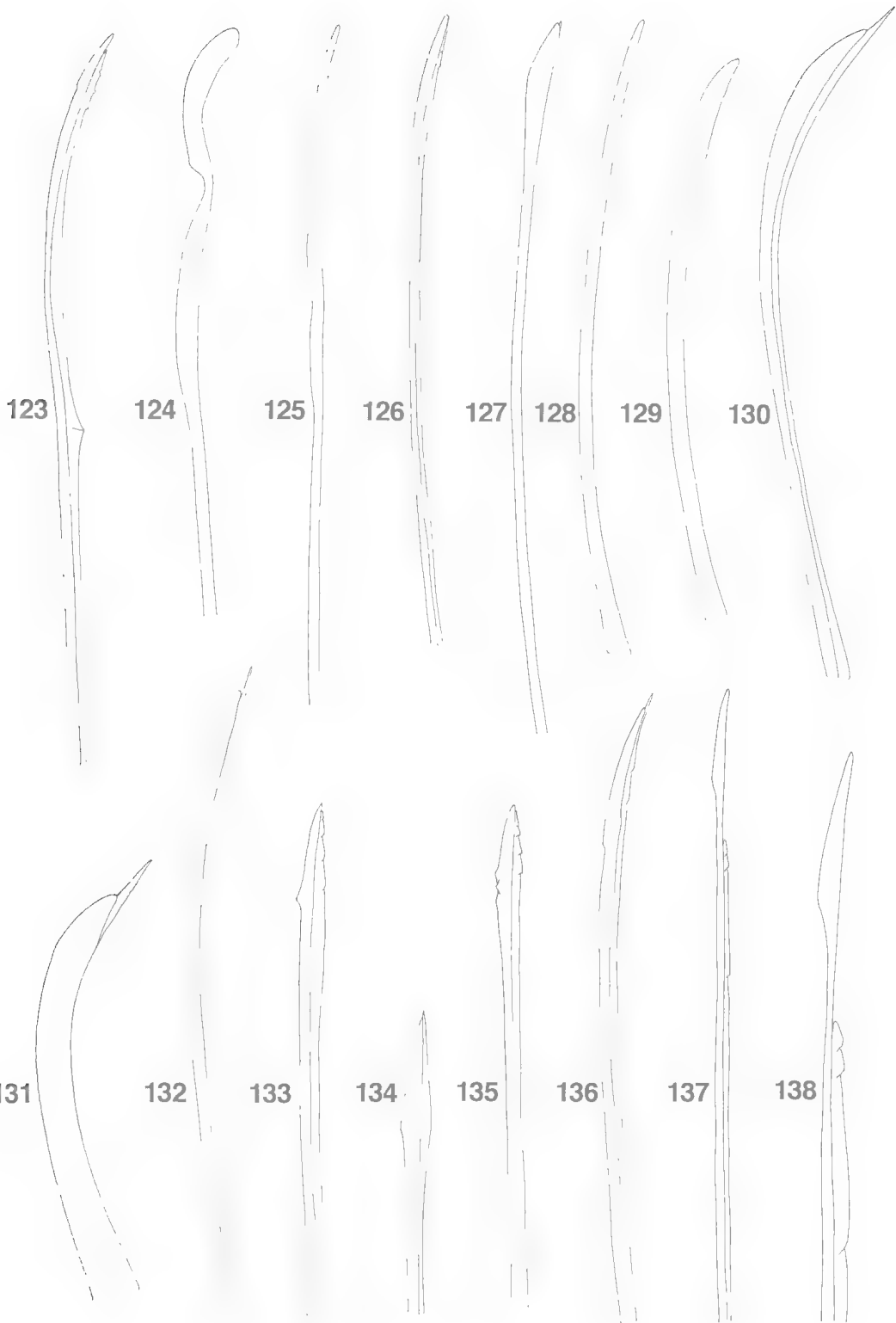
Vipiomorpha Tobias
(Fig. 16)

Although *Vipiomorpha* was originally described on the basis of a Russian species, *V. ypsilon* Tobias, apparently congeneric species occur in Africa and Australia. *Vipiomorpha* spp. are rather small members of the Glyptomorphini and are the only representatives of that tribe so far found in Australia, we know of a large number of undescribed species. Within the Glyptomorphini, *Vipiomorpha* is rather unspecialized and is probably fairly close to the basal stock of that tribe. Nothing is known of the biology of *Vipiomorpha* but other Glyptomorphini are predominantly parasitoids of concealed Coleoptera larvae.

Virgulibracon Quicke
(Figs 19, 65, 92, 137, 138)

Virgulibracon is a small genus of large, entirely Australian wasps. Nothing is known of the biology of the type-species, *Virgulibracon vulsus* Quicke. However, *V. endoxylaphagus* sp. nov., is a common and widespread species that parasitizes larvae of the cossid moth *Endoxyla* (= *Xyleutes* of Authors), which bores in *Eucalyptus* trunks and branches (see above). We have seen specimens of apparently the same species from all over Australia but, because some differences in coloration have been observed, it is possible that there may be several similar species involved. In addi-

FIGS 123-138. Features of the ovipositor: 123, *Ligulibracon* sp.; 124, *Cedilla cedilla* Quicke; 125, *Undabracon* sp.; 126, *Curriea* sp.; 127, *Paranesaulax* sp.; 128, *Hybogaster* sp.; 129, *Iphiaulax* sp.; 130, *Pycnobraconoides froggattii* (Cameron) n. comb. 131, *Stigmatobracon* sp. 132, *Psittacibracon lacteolus* Quicke; 133, *Mothibracon bimar*is (Turner); 134, *Africadesha tobiasi* sp. nov.; 135, *Eunesaulax terebratus* Tobias; 136, *Eunesaulax* sp.; 137, 138, *Virgulibracon endoxylaphagus* sp. nov., paratype, lower valves retracted



tion, several other undescribed species vary in the number of hamuli on hindwing vein C+SC+R, wing and metasomal coloration and the development of a spur from forewing vein 3-CU1. These wasps bore through solid wood to a depth of more than 4cm to reach their hosts (see van Achterberg, 1986).

Key to species of *Virgulibracon*

1. Metasoma, fore and mid legs and pterostigma entirely black; ovipositor (part exerted beyond apex of metasoma) less than 2.25 times longer than forewing *V. vulsus* Quicke
- Metasomal tergites 1-3 (at least) fore and mid legs and pterostigma orange to brownish orange; ovipositor (part exerted beyond apex of metasoma) more than 2.35 times length of forewing *V. endoxylaphagus* sp.nov.

Virgulibracon endoxylaphagus sp.nov. (Figs 19, 92, 137, 138)

MATERIAL EXAMINED

HOLOTYPE: ♀ with following data label: 'St Lucia, S.E. Queensland 8 Sep 1990. Ovipositing into *Endoxyla* (=Xyleutes of Authors) cinereus prepupa'. Deposited in QMBA.

PARATYPES: 3 ♀ ♀ with same data as holotype, 2 ♀ and 11 ♂ paratypes with following data label: 'St Lucia S.E. Queensland, 1 Sep 1990, G.B. Monteith. Emerging from Xyleutes Hole in 6' *Eucalyptus tereticornis* at 9.00 am'. All in QMBA except 1 ♀ and 1 ♂ in Quicke Collection, Sheffield.

DESCRIPTION (♀ ♀)

Length of body, 14.5-16.5mm, of forewing 16.0-17.0mm and of ovipositor 41-47mm.

Antenna with approximately 95 flagellomeres. Terminal flagellomere partly fused to the penultimate flagellomere. First flagellomere 1.5 and 1.8 times longer than the 2nd and 3rd flagellomeres respectively. 3rd flagellomere approximately as long as wide. Malar area shallowly depressed, finely coriaceous. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0:6.0:3.8; clypeus without a transverse median carina, the lower part curved inwards to form roof of hypoclypeal depression. Face shiny with some punctuation. Height of eye: width of face: width of head = 1.0:1.36:2.5. Face 2.27 times wider than high. Frons weakly impressed with a deep mid-longitudinal sulcus. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocell-

lus and eye = 1.5:1.0:2.75. Length of head behind eye: horizontal length of eye = 1.0:1.82.

Mesosoma approximately 1.47 times longer than high. Mesopleuron largely setose. Scutellar sulcus finely crenulate.

Forewing. Lengths of veins SR1:3-SR:r = 7.7:4.6:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.37:2.8:1.0. Vein 1-SR+M with well-developed spur. Vein cu-a marginally postfurcal. Vein 3-CU1 weakly expanded posteriorly. Vein CU1a with a small anteriorly directed spur near its apex.

Hindwing. Vein 2-SC+R. Apex of vein C+SC+R with one especially thickened bristle. Vein R1 with 3 or 4 proper hamules. Base of wing with a large glabrous area.

Lengths of fore femur: tibia: tarsus = 1.0:1.2:1.1. Lengths of hind femur: tibia: basitarsus = 1.52:2.65:1.0. Hind tibia slender; with a distinct longitudinal lateral groove. Hind basitarsus 9.2 times longer than deep.

Metasoma smooth and shiny. Antero-lateral parts of 2nd tergite and posterior margins of 3rd to 7th tergites membranous. Second tergite 1.3 times wider posteriorly than medially long. Ovipositor approximately 4 times longer than metasoma, 2.5 times longer than forewing.

Brown-orange except for the following which are black: antennae, mesosoma, hind legs, most of metasomal tergites 4-7, ovipositor sheaths. Membranous posterior margins of tergites 3-7 pinkish white. Basal third of wings pale yellowish, apical two thirds smoky; venation largely dark brown but C+SC+R and pterostigma orange.

DESCRIPTION (♂ ♂)

Males are smaller than females; body length 11-13mm.

Virgulibraconoides Quicke (Fig. 4)

A medium-sized genus of medium-sized wasps, which has been previously confused with *Callibracon* (see e.g. Ashmead, 1900), although they are not closely related. Probably the majority of species, all of which appear to be Australian, are undescribed.

Vomeribracon Quicke (Figs 66, 90, 108)

A small genus of medium-sized to large wasps occurring in Australia (north Queensland) and Papua New Guinea. Nothing is known of the biology of the only Australian species, *V. ingres-*

sor (Turner). However, an undescribed species from Papua New Guinea is an important larval parasitoid of the curculionid, *Pantorytes szentivanyi*, which is an important pest of cocoa (G. Holloway, pers. comm.).

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THE TADPOLES OF TWO QUEENSLAND FROGS (ANURA: HYLIDAE, MYOBATRACHIDAE)

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The tadpoles of two Queensland frogs, *Cyclorana brevipes* and *Uperoleia mimula*, are described and illustrated. *C. brevipes* is similar to previously described *Cyclorana*, having a rotund body and a 2(2)/3(1) tooth row formula. *U. mimula* shares with *U. lithomoda* an extremely small oral disc, a tooth row formula of 2(2)/3, and a black tail tip. □ *tadpoles, Hylidae, Myobatrachidae, Cyclorana brevipes, Uperoleia mimula, Queensland*

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Despite increased interest in Queensland's anuran fauna, the larvae of many species remain unknown. Given current concern about the conservation status of many species (Tyler, 1991; Wyman, 1990), accurate identification of larvae is important. The ability to identify larvae simplifies determination of the distribution and abundance of species, and is necessary for elucidation of their ecologies and life histories.

During research on frog communities in savanna woodland near Townsville, we collected amplexing pairs of two frogs whose larvae were unknown; the hylid *Cyclorana brevipes* and the myobatrachid *Uperoleia mimula*. These frogs were returned to the laboratory where oviposition occurred and larvae were reared to metamorphosis. In this paper we describe and illustrate the tadpoles of these species.

METHODS

Amplexant frogs transported to the laboratory were placed in large glass aquaria with 2-3cm of water at 25°C. Oviposition occurred within 12 hrs. When *C. brevipes* embryos reached stage 23 (Gosner, 1960) they were placed in 1000 litre plastic cattle tanks on the James Cook University campus. These tanks were assembled as described by Hearnden (1992), and supported a complex aquatic community similar to those found in temporary pools in the Townsville area, but lacking other anurans and most predators. Water temperature in the tanks ranged from 20-34°C. *U. mimula* tadpoles were reared for several weeks under artificial conditions in the laboratory prior to placement in the tanks, so no attempt was made to estimate larval period for this species.

Preserved specimens were measured using a dissecting microscope with an eyepiece micrometer. Terminology follows Altig (1970) and McDiarmid & Altig (1989). All measurements are in millimetres. Measurements involving apertures were taken from the centre of the aperture. The staging system is that of Gosner (1960). Specimens are lodged in the tadpole collection of the Zoology Department, James Cook University.

Cyclorana brevipes (Figs 1,2)

An amplexing pair was collected in a ditch at the intersection of Black River Road and Bruce Highway, 20km north of Townsville, Qld. on the evening of 2/3/90. Oviposition occurred before 0800 on 3/3/90 ($n = 930$ eggs), and embryos reached stage 23 by 5/3/90. The first metamorph (stage 46), observed on 28/3/90, measured 23.0mm snout to vent length and weighed 1.26g. The minimum total duration of development (fertilization to metamorphosis) was 25 days.

A stage 37 tadpole has the following measurements (millimetres): 56.0 total length, 22.5 body length, 4.5 basal tail muscle height, 3.5 basal tail muscle width, 2.8 maximum dorsal fin height located 10.8 from body terminus, 2.5 maximum ventral fin height located 11.0 from body terminus, 11.8 maximum body width, 10.8 maximum body height, 2.5 eye diameter, 0.9 pupil diameter, 7.2 interorbital distance, 0.5×0.3 narial diameters, 2.9 internarial distance, 3.2 snout-naris, 6.4 snout-eye, 11.8 snout-spiracle, 3.3 naris-eye, and 5.4 transverse oral disc diameter.

The oral disc is anteroventral and non-emarginate. The marginal papillae are in a single row

ventrally, with a wide gap dorsally and additional submarginal papillae laterally and dorsolaterally. The labial tooth row formula is 2(2)/3(1). The jaw sheaths are keratinized, the lower jaw sheath broad and V-shaped, and the upper jaw sheath narrow and curved (Fig. 1). The serrations on the margin of the upper jaw sheath are much finer than those on the lower jaw sheath.

The body is rotund, the snout is rounded in dorsal view, and the eyes are dorsolateral. The nares are dorsal and oriented anterolaterally. The sinistral spiracle is short and unpigmented, is almost ventral, and is not visible in dorsal view. The vent tube is short and dextral. The dorsal fin is not arched, and tapers to a narrow point posteriorly. It originates slightly anterior to the junction of the body and the tail musculature (Fig. 2). Dark pigmentation deep in the skin layers covers the intestinal coil dorsolaterally, from a line just posterior to the eyes. Lighter, diffuse brown pigmentation occurs on the rest of the body, tail muscle and fins. A patch of darker pigmentation almost surrounds the nares, with a lateral gap.

Uperoleia mimula
(Figs 3,4)

An amplexing pair was captured at an overflow area of a small creek near Bentley Dam, approximately 20km south of Townsville, in March 1990. A stage 38 specimen has the following measurements: 20.2 total length, 10.0 body length, 2.3 basal tail muscle height, 1.7 basal tail muscle width, 1.9 maximum dorsal fin height located 3.8 from body terminus, 1.3 maximum ventral fin height located 4.8 from body terminus, 6.6 maximum body width, 5.4 maximum body height, 1.4 eye diameter, 0.4 pupil diameter, 2.9 interorbital distance, 0.4 narial diameter, 1.3 internarial distance, 1.1 snout-naris, 2.4 snout-eye,

8.0 snout-spiracle, 1.4 naris-eye, 1.6 transverse oral disc diameter.

The oral disc is extremely small, located anteroventrally, and is non-emarginate. The jaw sheaths are narrow and keratinized. The labial tooth row formula is 2(2)/3. The short P3 tooth row is supported on an unusual flexible flap. Large marginal papillae in a single row surround the disc, with a large anterior gap and a narrow posterior gap (Fig. 3). The snout is rounded in dorsal view and the eyes are dorsal. The nares are located dorsally and open almost verically.

The body is slightly flattened dorsoventrally, and is oval when viewed from above. The spiracle is sinistral, located laterally and near the posterior of the body. It is extremely short, lightly pigmented, and oriented posteriorly (Fig. 4). The anus is dextral. Diffuse brown pigment occurs on the dorsal and lateral surfaces of the body, and on the tail muscle. Pigmentation on the fins is concentrated at the posterior tip in tadpoles that have not reached stage 31, forming a conspicuous black 'flag' that occupies approximately the most posterior 15-20% of the tail. From about stage 31 the pigment gradually disperses, until at stage 36 the 'flag' is hardly visible.

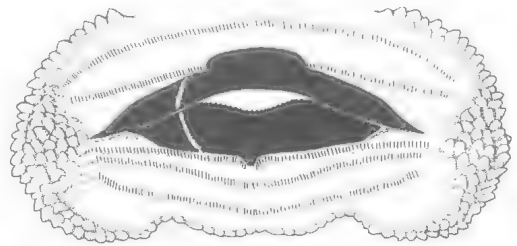


FIG. 1. Oral disc of *Cyclorana brevipes*. Scale bar = 1mm.

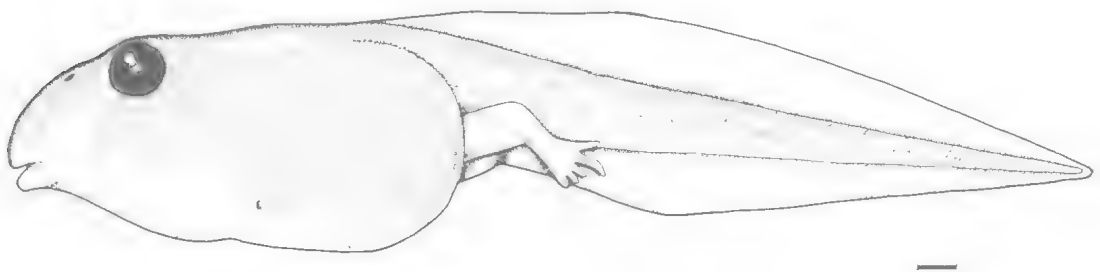


FIG. 2. Lateral view of a stage 37 *Cyclorana brevipes*. Scale bar = 2mm.

DISCUSSION

The tadpole of *Cyclorana brevipes* is difficult to distinguish from other *Cyclorana* previously described (Tyler & Martin, 1975; Tyler et al., 1982; Tyler et al., 1983; Watson & Martin, 1973). All have rotund bodies, tooth row formulae of 2(2)/3(1), and similar configurations of oral papillae. Tyler et al. (1983) were unable to distinguish tadpoles of *C. australis* from *C. longipes* when they occurred together in ponds in the Northern Territory, until the distinctive dorsal pattern of *C. longipes* appeared near metamorphosis. The tadpoles of these species reached different maximum sizes, but this character is only useful if late stage tadpoles are available for comparison.

Because of the extreme morphological conservatism displayed by this genus, accurate identification of Queensland tadpoles can best be achieved by the construction of regional keys that compare only the species found in a given area. The similarities in oral morphology exhibited by *Cyclorana* tadpoles will make knowledge about colour in life (and in preservative), and about size differences during development, fundamental for accurate identification. Knowledge about

Queensland *Cyclorana* is insufficient for such keys to be constructed at this stage.

Over 20 species of *Uperoleia* are now known to occur in Australia (Davies et al., 1986). However, information on the larval morphology of *Uperoleia* species is available for only four species, so meaningful comparisons are difficult. Two species, *U. inundata* (Tyler et al., 1983) and *U. lithomoda* (Davies et al., 1986) share with *U. mimula* a tooth row formula of 2(2)/3. *U. lithomoda* also shares with *U. mimula* a black tail tip. *U. laevigata* (as *U. marmorata*) is reported to lack gaps in any of the toothrows and has a formula of 1/3 (Moore, 1961). *U. tyleri* (as *U. marmorata*) differs from *mimula* in having a gap in the P1 tooth row (Watson & Martin, 1973).

None of these authors mention the unusual flap supporting the P3 tooth row. However the illustration of *U. inundata* in Tyler et al. (1983) suggests that this structure may be present in that species, and careful examination of other species may reveal its presence. The morphology and function of this structure require further study, as does the possibility that it may be a generically diagnostic feature.

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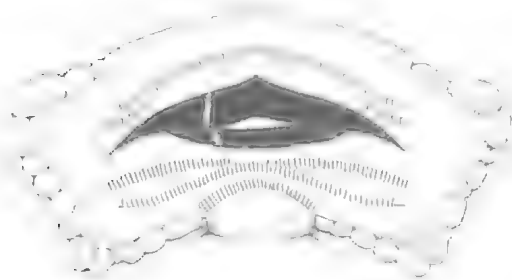


FIG. 3. Oral disc of *Uperoleia mimula*. Scale bar = 2mm.

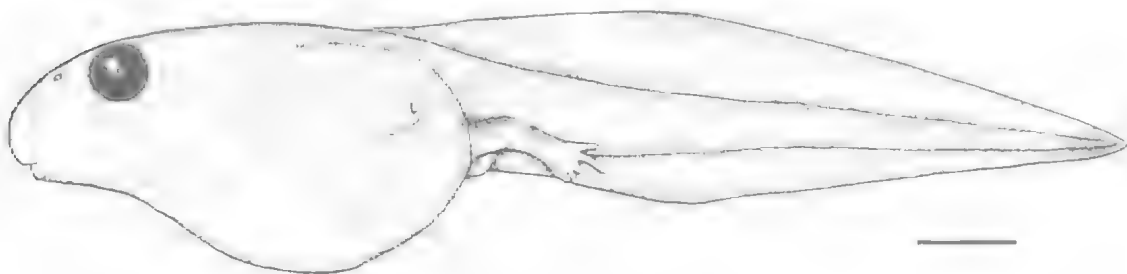


FIG. 4. Lateral view of a stage 38 *Uperoleia mimula*. Scale bar = 2mm.

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A NEW TWO-TOED SKINK FROM EASTERN AUSTRALIA

G.J. INGRAM, P.J. COUPER AND S.C. DONNELLAN

Ingram, G.J., Couper, P.J. & Donnellan, S.C. 1993 06 30: A new two-toed skink from eastern Australia. *Memoirs of the Queensland Museum* 33(1): 341-347, Brisbane, ISSN 0079-8835.

Lerista emmotti sp.nov. has been confused with *L. punctatovittata* (Günther, 1867). However, it differs from *L. punctatovittata* in the state of the forelimb (distinctly didactyle vs monodactyle or monostylus). As well, it can be distinguished by estimates of genetic distance derived from allozyme electrophoresis. □ *Scincidae*, *Lerista emmotti*, *Lerista punctatovittata*, new species, electrophoresis, Australia.

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When Couper & Ingram (1992) described *Lerista colliveri*, they were aware of another probable species of *Lerista* that had been confused with *L. punctatovittata*. It differed in the state of the forelimb (distinctly didactyle vs monodactyle or monostylus). However, no other morphological characteristics that differentiated them were found. As well, the different states of the limb did not appear to be a good enough reason to describe a new species. Degenerate-limbed skinks may vary in the extent of development of the toes, and the different conditions are more valuable in the study of embryology than as characters for differentiating taxa. However, subsequent work by one of us (SCD) showed that the two-toed individuals could be distinguished by estimates of genetic distance derived from allozyme electrophoresis.

Queensland Museum's specimens are prefixed by QMJ, Australian Museum's by AMR and South Australian Museum's by SAMAR.

ELECTROPHORESIS

MATERIALS AND METHODS

Twenty-seven '*Lerista punctatovittata*' were collected from 11 localities in Queensland, New South Wales and South Australia. Livers were dissected from fresh specimens and stored at -80°C until use. For the genetic analysis, specimens from a single locality which showed all the expected genotypes at each locus were treated as a population of a single genetic type. On this basis, 11 populations were designated:

NOON – Noonbah Station, Qld (24°07'S, 143°11'E) (QMJ54144-6);

STON – Waterloo Station, via Stonehenge, Qld (24°16'E, 143°17') (QMJ56312-4);

KAKA – Ka Ka Mundi, Qld (24°49'E, 147°24'S) (QMJ56090);

NYMA – Nymagee, NSW (32°01'E, 146°20'S) (SAMAR33548-50/552-7);

MTHO – Mt Hope, NSW (32°51'E, 145°53'S) (SAMAR33522);

CHOW – Chowilla, SA (33°56'E, 140°59'E) (SAMAR32991-2, 33003);

POOG – Pooginook CP, SA (34°04'E, 140°07'S) (SAMAR38345/352);

WAIK – 2km S Waikerie, SA (34°12'E, 140°01'S) (SAMAR39731);

BROO – Brookfield CP, SA (34°19'E, 139°30'S) (SAMAR36974);

WIDA – 11km S Widara HS, SA (34°20'E, 139°57'S) (SAMAR38442)

BOON – 4.5km E Boongalechie, SA (34°27'S, 139°26'E) (SAMAR39267).

Homogenates of liver were electrophoresed on sheets of cellulose acetate (Cellogel; Chemetron) as described by Richardson et al. (1986), and were assayed for 35 enzymes which were encoded by 40 presumptive loci. The enzymes stained, E.C. numbers and abbreviations (Murphy et al., 1990) are: aspartate aminotransferase (AAT, E.C. 2.6.1.1), aconitate hydratase (ACOII, E.C. 4.2.1.3), aminoacylase (ACYC, E.C. 3.5.1.14), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), adenylate kinase (AK, E.C. 2.7.4.3), alanine aminotransferase (ALAT, E.C. 2.6.1.2), carbonate dehydratase (CA, E.C. 4.2.1.1), leucine aminopeptidase (CAP, E.C. 3.4.11.1), enolase (ENO, E.C. 4.2.1.11), fructose-diphosphatase (FBP, E.C. 3.1.3.11), fumarate hydratase (FUMH, E.C. 4.2.1.2), glyceraldehyde-phosphate dehydrogenase (GAPDH, E.C. 1.2.1.2), guanine deaminase (GDA, E.C. 3.5.4.3), glycerol-3-phosphate dehydrogenase (G3PDH, E.C. 1.1.1.8), glucose-6-phosphate dehydrogenase (G6PDH, E.C. 1.1.1.49), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), glutathione reductase (GR, E.C. 1.6.4.2), glutamate dehydrogenase (GTDH, E.C. 1.4.1.3), L-idoitol dehydrogenase (IDDH, E.C. 1.1.1.14), isocitrate dehydrogenase (IDH, E.C.

TABLE 1. Electromorph frequencies, expressed as a percentage, in 11 populations of '*Lerista punctatovittata*' at 40 loci. Electromorphs are designated alphabetically, with 'a' being the most cathodally migrating electromorph. Where enzymes are encoded by more than one locus, the loci are designated numerically in order of increasing electrophoretic mobility. Where the electromorph frequencies are not given, the frequency is 100. See 'Material and Methods' for an explanation of the population codes. The number of individuals sampled from each population is given under each locus. The following loci were invariant: *Aat-1*, *Aat-2*, *Acoh-1*, *Acyc*, *Adh*, *Ak-1*, *Ak-2*, *Ca*, *Cap*, *Eno*, *Fumh*, *Gapdh*, *Gda*, *G3pdh*, *Gpi*, *Gidh*, *Iddh*, *Ldh-1*, *Ldh-2*, *Lgl*, *Mdh-1*, *Mdh-2*, *Mpi*, *Pgam*, *Pk* and *Sod*.

LOCUS	STON	NOON	KAKA	MTHO	NYMA	CHOW	BROO	POOG	WIDA	BOON	WAIK
<i>Acoh-2</i>	e(50)	f(33)	d	d	d	d	d	d	d	d	d
	a(50)	c(17)									
		b(33)									
		a(17)									
<i>Alat</i>	3	3	1	1	10	3	1	2	1	1	1
	b	a	a	a	a	a	a	a	a	a	a
	2	3	1	1	10	3	1	2	1	1	1
<i>Fbp</i>	a	a	a	b	b	b	b	b	b	b	b
	3	3	1	1	10	3	1	2	1	1	1
<i>G6pdh</i>	b(17)	b(33)	a	a	a	a	a	a	a	a	a
	a(83)	a(67)									
	3	3	1	1	10	3	1	2	1	1	1
<i>Gr</i>	a	b(50)	a	-	a	a	a	a	a	-	a
		a(50)									
	2	2	1	0	10	3	1	2	1		1
<i>Idh</i>	a	b(33)	a	b	b(35)	b(50)	b	b(50)	b	b	b(50)
		a(67)			a(65)	a(50)		a(50)			a(50)
	1	3	1	1	10	3	1	2	1	1	1
<i>Mdhp</i>	a	a	a	b	b(85)	b(67)	b(50)	b	b	b	b
					a(15)	a(33)	a(50)				
	3	3	1	1	10	3	1	1	1	1	1
<i>PepA</i>	b	b(50)	b	b	b(80)	b	b	b(75)	b	b	b
		a(50)			a(20)			a(25)			
	3	3	1	1	10	3	1	2	1	1	1
<i>PepB</i>	c(33)	b	b	b(50)	b	b(83)	b(50)	b	a	b(50)	b(50)
	b(67)			a(50)		a(17)	a(50)			a(50)	a(50)
	3	3	1	1	10	3	1	2	1	1	1
<i>PepD</i>	a	b	a	a	a	a	-	a	a	a	a
	3	2	1	1	10	3		1	1	1	1
<i>Pgdh</i>	b	a	b	b	b	b	-	b	b	b	b
	3	3	1	1	10	3		1	1	1	1
<i>Pgm-1</i>	a	b(67)	b	b	b(61)	b(67)	b(50)	b(50)	a	b(50)	b(50)
		a(33)			a(39)	a(33)	a(50)	a(50)		a(50)	a(50)
	3	3	1	1	9	3	1	1	1	1	1
<i>Pgm-2</i>	a	a	b(50)	a	a	a	a	a	a	a	a
			a(50)								
	3	3	1	1	10	3	1	2	1	1	1
<i>Tpi</i>	a	a	a	a	a	a	a	a	b(50)	a	a
									a(50)		
	3	3	1	1	10	3	1	2	1	1	1

1.1.1.42), lactate dehydrogenase (LDH, E.C. 1.1.1.27), lactoyl-glutathione lyase (LGL, E.C. 4.4.1.5), malate dehydrogenase (MDH, E.C. 1.1.1.37), 'malic' enzyme (MDHP, E.C. 1.1.1.40), mannose-phosphate isomerase (MPI, E.C. 5.3.1.8), peptidases (PEP, E.C. 3.4.11 or 13.*), phosphoglycerate mutase (PGAM, E.C. 5.4.2.1), 6-phosphogluconate dehydrogenase (PGDH, E.C. 1.1.1.44), phosphoglucomutase (PGM, E.C. 2.7.5.1), pyruvate kinase (PK, E.C. 2.7.1.40), superoxide dismutase (SOD, E.C. 1.15.1.1), and triose-phosphate isomerase (TPI, E.C. 5.3.1.1). Electromorphs were identified by comparison with samples that were

repeatedly included on each gel (internal controls) and through critical side-by-side comparisons (line-ups; see Richardson et al., 1986).

RESULTS

Electromorph distributions at the 40 loci resolved are shown in Table 1. These data were converted into a matrix of percentages of loci showing fixed differences between populations (Table 2). A fixed difference occurs at a locus when the two populations being compared share no electromorphs (Richardson et al., 1986). Figure 1 is a phenogram of the percentage fixed differences between populations, constructed by the unpaired group method of analysis (UPGMA). The phenogram is not intended to reflect phylogenetic relationships, but rather to give a visual indication of the genetic diversity and genetic distances between the 11 populations. The specimens fell into three major genetic groups: 1, Stonehenge; 2, Noonbah; and 3, Ka Ka Mundi and the populations from NSW/SA.

The Stonehenge and Noonbah populations are regionally sympatric (separated by 15km) and have fixed differences at 3 loci (*Gpt*, *PepD* and *Pgdh*). The Ka Ka Mundi/NSW/SA populations have fixed differences with Stonehenge and Noonbah at a minimum of 3 (*Acoh-2*, *Alat* and *Fbp*) and 2 loci (*Acoh-2* and *Fbp*; *PepD* and *Pgdh* not scored in Brookfield population) respectively. Within the Ka Ka Mundi/NSW/SA group, Ka Ka Mundi has a single fixed difference (*Fbp*) with the NSW/SA populations.

From the preceding electrophoretic analysis, the Noonbah population is clearly distinct from the other populations. Morphologically, all the Noonbah specimens have a didactyl forelimb while the specimens from the other populations have a monodactyl or monostylar forelimb. The latter are identifiable with *L. punctatovittata* and the Noonbah specimens thus warrant recognition as members of a new species.

SYSTEMATICS

Lerista emmotti sp.nov. (Figs 2-4)

1992 *Lerista punctatovittata* (in part); Cogger, 1992.

MATERIAL EXAMINED

HOLOTYPE: QMJ53959 Noonbah Stn, 140km S of Longreach (24°07'S, 143°11'E), CQ, A. Emmott, 2 September 1991.

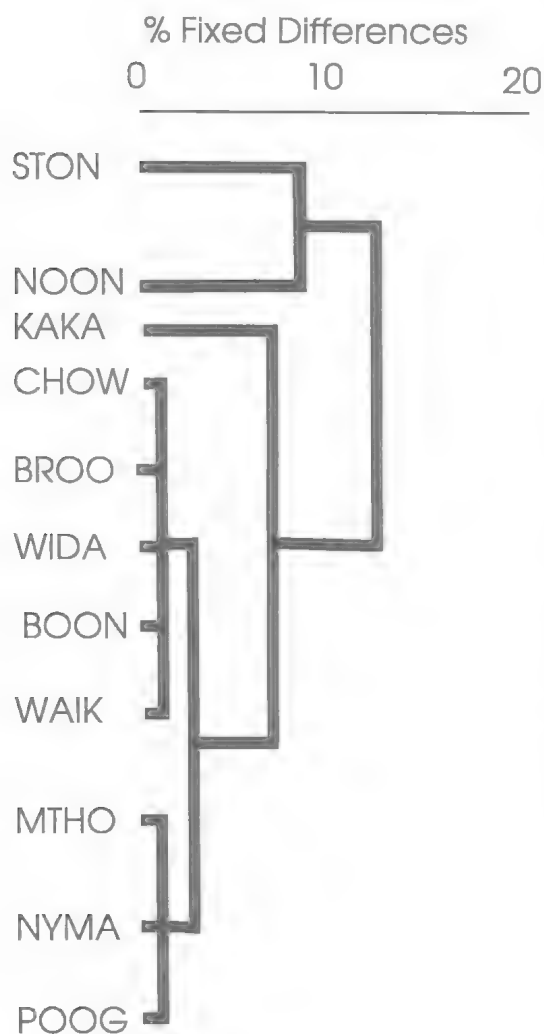


FIG. 1. Phenogram of the percentage fixed differences between populations, constructed by the unpaired group method of analysis (UPGMA).



FIG. 2. *Lerista emmotti* sp. nov., paratype QMJ51630 in life, Noonbah Station, CQ (Steve Wilson).

PARATYPES: QMJ9038 Muttaburra (22°36'S, 144°33'E), CQ; QMJ54491-2 Hickleton Stn (24°02'S, 143°08'E), CQ; QMJ50066, 50068-69, 51217-8, 51629-30, 52585-7, 53958, 53960, 54144-6, 54292, 54493 Noonbah Stn (24°07', 143°11'), CQ; QMJ 51529, no data; AMR92302 Woollana Homestead (30°25'E, 139°25'S), SA; AMR14682, Mootwingee Water Holes (31°17'E, 142°18'S), NSW; AMR114408 north end of Mungo Homestead airstrip, Mungo NP (33°43'S, 142°57'E), NSW; AMR114314 Old Arumpo Homestead (33°48'S, 142°53'S), NSW.

DIAGNOSIS

A large (maximum snout-vent length 103mm) *Lerista* with a movable eyelid and didactyl fore- and hindlimbs. A member of the *L. macropis-thopus* species group (cf. Wilson & Knowles, 1988), of which the following members may also be didactyle on both fore- and hindlimbs: *L. gerrardii*, *L. neander* and *L. picturata*. *L. emmotti* is readily distinguished from *L. gerrardii* by pattern (broad black upper lateral stripe absent vs broad black upper lateral stripe present); from *L. nean-*

TABLE 2. Matrix of percentage fixed allelic differences between 11 populations of '*Lerista punctatovittata*'

	STON	NOON	KAKA	MTHO	NYMA	CHOW	BROO	POOG	WIDA	BOON	WAIK
STON	-										
NOON	8	-									
KAKA	8	8	-								
MTHO	15	13	8	-							
NYMA	8	10	3	0	-						
CHOW	8	10	3	0	0	-					
BROO	13	7	7	0	0	0	-				
POOG	10	13	5	0	0	0	0	-			
WIDA	15	15	14	3	3	0	0	3	-		
BOON	14	14	8	0	0	0	0	0	0	-	
WAIK	10	13	5	0	0	0	0	0	0	0	-



FIG. 3. *Lerista emmotti* sp. nov. (paratype QMJ51218). Above: dorsal view of head. Below: lateral view of head.

der by the number of supraciliaries (5 vs 3); from *L. picturata* by the number of supraciliaries (5 vs 1-3). *L. emmotti* most closely resembles *L. punctatovittata* but it can be separated from this species by the state of the forelimb (distinctly didactyle vs monodactyle or monostylus). *L. emmotti* is further distinguished from *L. punctatovittata* by the biochemical data in Table 1.

DESCRIPTION

Snout-vent length: 39-103mm (N 24, mean 72.6). Length of appendages etc. (% snout-vent length): forelimb 3-7 (N 24, mean 4.5), hindlimb 11-16 (N 24, mean 13.0), tail 87-122 (N 13, mean 105.2), head length 8-13 (N 24, mean 9.9), head width 6-9 (N 24, mean 6.9).

Nasal contact narrow (N 1) to moderate (N 20) to broad (N 5). Nostril positioned anteriorly to centrally on nasal scale. Rostral shield rounded in profile. Prefrontals small to moderate, widely spaced. Interparietal large and free. Frontoparietals narrowly (N 4) to moderately (N 22) spaced, smaller than interparietal. Parietals in narrow contact (N 1), moderate contact (N 3), broad contact (N 22). Enlarged nuchal scales 5-9 (N 14, mean 7.8), of which only two contact the parietals. Lower eyelid movable. Opaque disc occupying more than half the lower eyelid. Supraoculars 3, first two in contact with the frontal. Supraciliar-

ies 5 (N 26). Loreals 2, second usually smaller. Presuboculars 2. Supralabials 6, fourth below eye. Infralabials 5-6 (N 26, mean 5.9). Primary temporals 1. Secondary temporals 2, lower smallest and overlapping upper. Ear aperture minute, overlapped by scales. Midbody scale rows 18, rarely 20 (N 26, mean 18.3). Paravertebral scales 78-90 (N 24, mean 85.5). Two enlarged preanal scales (N 25); right overlapping left (N 14), left overlapping right (N 11). Forelimb with two digits; both digits clawed (N 19), only one digit clawed (N 6), neither digit clawed (N 1). Hindlimb with two clawed digits, 2nd digit markedly longer than 1st. Lamellae under longest toe 9-12 (N 26, mean 10.6).

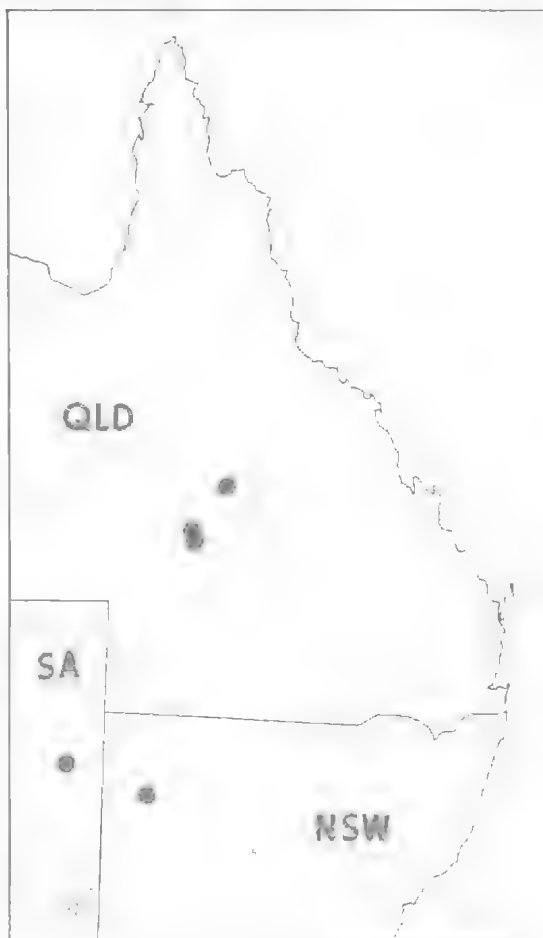


FIG. 4. Distribution of *Lerista emmotti* sp. nov. Numbers refer to populations of '*L. punctatovittata*' electrophoresed: 1, Noon; 2, Ston; 3, Kaka; 4, Nyma; 5, Miho; 6, Chow; 7, Poog; 8, Waik; 9, Broo; 10, Wida; 11, Boon.

Dorsal and upper lateral ground colour tan to mid-brown with the each scale bearing a dark streak, which in turn form longitudinal lines of dark spots. Mid to lower lateral zone cream, marked by dark flecks. Venter either immaculate cream, or sometimes obscurely marked by dark-edged scales. Under surface of tail faintly to strongly patterned with dark flecks. Head shields dark-edged; lips barred; loreals and temporals marked by a dark streak which breaks up posteriorly.

DISTRIBUTION

From Muttaborra (22°36'E, 144°33'S), central Queensland, southwest to old Arumpo homestead, (33°48'E, 142°53'S), New South Wales. Also extending into South Australia (30°25'E, 139°25'S).

ETYMOLOGY

Named for Angus Emmott, naturalist and friend of the Queensland Museum.

REMARKS

Our examination of the holdings of the Queensland and Australian Museums showed '*L. punctatovittata*-like' *Lerista* with didactyl forelimbs to be confined to the western edge of the known distribution of *L. punctatovittata*. These specimens, described here as *L. emmotti*, are both morphologically and biochemically distinct from *L. punctatovittata*. However, monostylar individuals from central Queensland, which appear to be morphologically indistinguishable from *L. punctatovittata*, are biochemically distinct from the more easterly and southerly populations of this species.

Clearly, *L. punctatovittata* as currently recognised is a composite species. Unfortunately the locality given for the holotype is simply 'Queensland'. Although it is tempting to assume that this specimen was most likely collected from more coastal populations, such an assumption would be unsound because considerable settlement of western Queensland had taken place by the time *L. punctatovittata* (Günther, 1867) was described. The distribution of *L. punctatovittata* and the description of cryptic forms within this species complex warrant further investigation.

As well, even though we have assigned didactyl specimens from NSW/SA to *L. emmotti*, nevertheless the possibility remains that some populations of *L. punctatovittata* are polymorphic for the didactyl-monodactyl condition. This possibility should be tested by further allozyme analysis.

The holotype of *L. punctatovittata* (Natural History Museum, London BMNH 1946.8.18.80; Cogger et al, 1983) has a monostylar forelimb (Boulenger, 1887) and is not a specimen of *L. emmotti*. Cogger et al. (1983) listed *Rhodona officieri* McCoy, 1881, as a junior synonym of *L. punctatovittata* and noted that the type material of *officieri* had not been located (see also Coventry, 1970). However, McCoy's description and illustration of the holotype are detailed. The specimen agrees in all characteristics with *L. punctatovittata*, including having a monodactyl forelimb. We therefore concur with the synonymy of Cogger et al., (1983).

This study highlights the power of combining morphological character analysis with an independent genetic technique, such as allozyme electrophoresis, to assess the systematic significance of seemingly trivial morphological variation.

ACKNOWLEDGEMENTS

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NEW RECORDS OF THE RARE GREEN-THIGHED FROG. *Memoirs of the Queensland Museum* 33(1): 348. 1993:- The Green-thighed Frog (*Litoria brevipalmata*) is a mysterious frog, populations of which apparently suddenly appear and disappear at a locality—sometimes the 'absences' are for many years (Tyler & Davie, 1985). These disappearances, however, do not appear to be part of the phenomenon of the 'disappearing frogs' (sensu Czechura & Ingram, 1991) because the species is still extant.

Until recently, the Green-thighed Frog was known from only three locations in Queensland. McDonald (1974) collected a specimen at Crows Nest National Park (NP 629: 27°15'S, 152°06'E) and another from Ravensbourne National Park (NP 492: 27°21'S, 152°12'E). Four years later, the species was collected near Jimna (26°39'S, 152°27'E) (Czechura, 1978) and in 1983 Chris Corben collected two specimens (Queensland Museum [QM] J42134, 42135) also near Jimna. All these records are from montane country.

Recently the senior author collected two male Green-thighed Frogs alongside Woogaroo Creek near Wacol, Brisbane (27°36'S, 152°54'E). These are the first coastal records for this frog in Queensland and add to the frog fauna of the Brisbane area. These records are reported here. Frog names follow Ingram et al. (1993).

First collection, 21 November 1992

At Woogaroo Creek near Wacol, heavy rain, with lightning, began falling at about 4.30pm and by 5.00pm there were radio reports of local flooding. Rain then reduced to a steady light fall with intermittent heavier showers. Observations began at about 8.00pm at a large L-shaped depression ('Ric's Ditch'), some 40m in length, alongside Woogaroo Creek and some 30m from the main creek-line. From previous experience, this depression became an ephemeral pool after good rain. On the day before, considerable rain had fallen in the afternoon and evening but not enough to produce free-standing water. By contrast, the rainfall of the 21st resulted in 85cm of water at the deepest point of the depression.

Amongst the extremely loud chorus of a large number of frogs, an unfamiliar call was heard. This proved to belong to a male *L. brevipalmata*, which was immediately captured (QM J56813). Several more calling males were observed but not collected and, judging from their calls, about 20 males were present at the site; no females were observed. Typical calling sites were in leaf litter about 0.5–0.9m from the water's edge. No Green-thighed Frogs were found away from the depression.

The following species of frogs were also noted: *Limnodynastes oratus*, *L. peronii*, *Litoria caerulea*, *L. f. lax*, *L. eruehensis*, *L. rubella*, *Adelotus brevis* and *Mixophyes fasciolatus*. Curiously, although the Cane Toad (*Bufo marinus*) was seen well away from the site on a nearby sealed road, none was heard calling or seen in the depression despite what appeared to be ideal breeding conditions.

The vegetation surrounding Ric's Ditch is open dry sclerophyll forest with a sparse, predominately acacia understorey and a ground cover of exotic herbs and grasses. Closer to the creekline there is a heavy infestation of Chinese Elm (*Ulmus sinensis*), Camphor Laurel (*Cinnamomum camphora*), a dense understorey of Bush Lanata (*Lantana camara*) and a variety of native species that form depauperate, dry rainforest.

No frogs were observed at the site on the two following nights (22, 23 November), although calls of *Adelotus brevis* and *Lim-*

nodynastes peronii were heard. Within ten days, there was no follow-up rain and the depression became completely dry — all tadpoles apparently perishing.

From 21 November 1992 to 5 January 1993, some rain fell intermittently but not enough to produce any significant frog activity. However, on some occasions these falls were accompanied by, or quickly succeeded by, strong breezes and it is possible the accompanying noise hid the sounds of calling frogs. From 1 January 1993, rainfall was recorded near Ric's Ditch. On the evening of 4 January 1993, a very brief storm produced 0.6mm and on the next afternoon a more substantial storm resulted in 30mm. At Ric's Ditch, 30mm was insufficient to produce free-standing water. Apart from a brief call from a Naked Treefrog (*Litoria rubella*), the only active caller was the Red-backed Broodfrog (*Pseudophryne coriacea*), with about 30 frogs that called from small, natural tunnels in very porous substrate.

Second collection, 6 January 1993

In the late afternoon, a vigorous electrical storm resulted in a fall of 48.5mm and, by 8.00pm, a loud chorus of frogs came from Ric's Ditch. About a dozen Green-thighed Frogs were calling and another male was collected (QM J57285). The same species of frogs noted on 21 November 1992 were recorded again and Cane Toads were also absent.

The next day was overcast with occasional light rain. Very light rain was falling at about 7.30pm when Ric's Ditch was revisited. There were about twice as many males of Green-thighed Frogs calling compared to the night before and several of these were much closer to the water, with one about 10 cm from shallow water. As before, no females were observed.

An immediate visit was made to the neighbouring Six Mile Creek some 8km distant and observations were made at several sites. A slightly different frog fauna was recorded. *Litoria nasuta* and *Cinia parvinsignifera* were numerous in open grassy areas. In a melaleuca swamp, there were *Limnodynastes terraereginae* and *Litoria dentata*. In the Blacken Fern (*Pteridium esculentum*) the Dusky Gungan (*Uperoleia fusca*) was recorded. However, despite considerable searching over a wide area, the Green-thighed Frog was not found.

Since 6 January, until now (22 May 1993), the Green-thighed Frog has not been met with at Woogaroo Creek, despite repeated visits.

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- A.E.O. Nairns, 25 Warwick Court, Bellbird Park, Queensland 4300, Australia; Glen J. Ingram, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 22 May, 1993.

EARLY PERMIAN INADUNATE CRINOIDS FROM THAILAND

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Eight species of Early Permian inadunate crinoids are described from Ko Muk, Ko Phi Phi, and Ko Yao Noi, islands off southern Thailand. These are the first Palaeozoic crinoids described from Thailand and support an Early Permian age for the Phuket Group and Rat Buri Limestone. New species described are *Kallimorphocrinus thaiensis*, *Apographocrinus komukensis*, and *Contocrinus andamanensis*; five species are left in open nomenclature. □ Permian, crinoids, inadunate, Thailand.

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Permian rocks are widespread in Thailand (Waterhouse & Piyasin, 1970, fig. 1; Lumjuan & Lovacharasupaporn, 1984). Since 1960 systematic studies, including stratigraphic interpretations have concentrated on brachiopods (Yanagida, 1984), fusulinids (Toriyama, 1984; Ingavat, 1985), and bryozoans (Sakagami, 1984). This paper is the first to describe Permian crinoids from Thailand.

LOCATION AND STRATIGRAPHY

Crinoids were derived from five localities on the islands of Ko Muk, Ko Phi Phi, and Ko Yao Noi northwest of Kan Tang in the Andaman Sea off southern Thailand. Maps of the islands showing general position of fossil localities are as follows: 1, upper Phuket Group, SW side of Ko Muk, with stratigraphic sections (Waterhouse, 1982, figs 2b,3,4); 2, upper part of Phuket Group and 3, basal part of Rat Buri Limestone, Ko Phi Phi, indicated on measured section of Tong Lang Bay (Waterhouse, 1982, fig. 2a); 4, Rat Buri Limestone, Ko Muk, U.S. National Museum locality 9271 (Grant, 1976, fig. 7); and 5, Rat Buri Limestone, Ko Yao Noi, (Waterhouse et al., 1981), fig. 4. An unsuccessful attempt was made to locate the calyx reported by Waterhouse (1982, p. 339), from the Phuket Group on Ko Phi Phi for inclusion in this study.

In southern Thailand Phuket Group brachiopods are considered Sakmarian (Waterhouse et al., 1981; Waterhouse, 1982). The Rat Buri Lst has been considered Artinskian (Sakagami, 1970; Yanagida, 1970; Grant, 1976), late Early Permian (Yanagida, 1984). Kazanian (Waterhouse & Piyasin, 1970) or Kungurian (Waterhouse, 1981).

The Rat Buri Limestone has been applied somewhat indiscriminately to Permian lime-

stones throughout Thailand (Grant, 1976). Diversity of carbonate microfacies within the Rat Buri Limestone is reflected in the reports of many beds with restricted faunas, i.e., fusulinids with rare or no brachiopods or abundant brachiopods and bryozoans with no fusulinids (Grant, 1976). Fusulinids are virtually unknown in the Rat Buri Limestone in peninsular Thailand (Toriyama, 1984, fig. 1), but in central and northern Thailand fusulinids range from Sakmarian to Dorashamian (Ingavat, 1985). A Sakmarian ammonoid fauna occurs in the basal Rat Buri Limestone in central Thailand (Glenister et al. 1990). Waterhouse (1981) correlated the Rat Buri Limestone of southern Thailand with the Bitauai Beds of Timor. However, the Bitauai Beds are considered Artinskian based on ammonoids (Glenister & Furnish, 1987).

Considerable work remains in determining stratigraphic relationships of the Rat Buri Limestone throughout Thailand. However, sufficient palaeontological information is available to evaluate the age of the unit at most localities. Based on fusulinids and ammonoids the base of the Rat Buri Limestone in central and northern Thailand is Sakmarian or Artinskian. In peninsular Thailand we consider the Rat Buri Limestone to be of Artinskian age based on data of Sakagami (1984) and Yanagida (1984) and correlation of the brachiopod faunas with the Timorese Bitauai fauna (Grant, 1976; Waterhouse, 1981).

Clastic sediments of the Phuket Group have been referred to as cool water deposits equivalent to glaciomarine deposits of Gondwanaland (Waterhouse, 1982 among others). Altermann (1986) considered these deposits to represent deposition on a continental margin lacking sufficient evidence to interpret them as glaciomarine. Brachiopods from a carbonate band within the pebbly

mudstones in the upper part of the Phuket Group were interpreted by Waterhouse (1982) as mostly cool temperate genera. Brachiopods from the Rat Buri Limestone were interpreted (Grant, 1976) as tropical with marine connection to cooler water. Waterhouse (1982) considered the brachiopod faunas of the Rat Buri Limestone to have a stronger cool temperate composition.

FAUNAL SIGNIFICANCE

All crinoids reported are allagecrinid or advanced poterioecrinid cladids. The allagecrinid *Kallimorphocrinus* occurs in the Carboniferous and Permian in North America, the Carboniferous of Europe and Permian of Timor and Russia (Bassler & Moodey, 1943; Webster, 1973, 1977, 1986, 1988). *K. thaiensis* and *K.?* sp.nov. from the Phuket Group are related to Permian *Kallimorphocrinus* and *Wrightocrinus* from Timor.

The dorsal cup from the Phuket Group, assigned to *Cymbiocrinus* is the second report of the genus from the Permian and outside North America. Cymbiocrinids are considered the ancestral stock of the calceolispongiids, a Tethyan family restricted to the Permian of Australia, Timor and India (Moore & Strimple in Moore & Teichert, 1978). The bulbous basals of *Cymbiocrinus* are considered a continuation of the cymbiocrinid lineage in parallel with the calceolispongiids which had branched off earlier.

The other advanced poterioecrinids from the Rat Buri Limestone are small specimens, perhaps not fully mature. They belong to genera that are relatively small but typically larger than these specimens. *Apoglyphocrinus* is known from the Upper Carboniferous and Lower Permian of North America and the Permian of Russia, Timor and Western Australia (Bassler & Moodey, 1943; Webster, 1973, 1977, 1986, 1988). *A. komukensis* is most similar to *A. punilus* of the Early Permian Callytharra Formation of Western Australia (Webster, 1987) and Permian Basleo Beds of Timor (Wanner, 1916). The partial crown questionably assigned to *Apoglyphocrinus* has a more elongate cup than is typical in the genus. This may reflect immaturity as height:width ratio of the cup may decrease with growth as in other inadunates (Pabian & Strimple, 1985).

Contocrinus is known only from the Late Carboniferous and Early Permian of North America (Webster, 1973, 1977). The advanced condition of the anal interarea in *Contocrinus andamanensis* sp.nov. suggests a Permian age. The partial crown questionably assigned to the Clathrocrini-

dae has arm structure similar to the Late Carboniferous *Clathrocrinus* known only from North America (Webster, 1977, 1986). Cup features suggest advanced morphology common in Late Carboniferous or Permian poterioecrinids.

None of the three poterioecrinid genera from the Rat Buri Limestone are restricted to the Permian; they occur in the Late Carboniferous and Permian or Late Carboniferous only. The lack of strong ornament on the cladids may indicate they are farther offshore or deeper water forms (Pabian & Strimple, 1985). Preservation of crowns with proximal columnals attached implies little if any postmortem transport.

Crinoid ossicles are common elements with brachiopods and bryozoans in shallow shelf carbonates and marls in the late Palaeozoic (Lane & Webster, 1980; Pabian et al., 1989). All Thai crinoids discussed were associated with brachiopods and bryozoans. However, crinoids were sparse in residues from the Phuket Group and the Rat Buri Limestone. Some samples were totally lacking in crinoidal debris. This is considered a reflection of some paleoecologic control, perhaps water temperature.

SYSTEMATIC PALAEOONTOLOGY

Morphologic terminology follows Moore & Teichert (1978). Specimens are deposited in the: United States Nation Museum (USNM), University of Tasmania (UT) and University of Queensland (UQ)

- Class CRINOIDEA Miller 1821
- Subclass INADUNATA Wachsmuth & Springer, 1885
- Order DISPARIDA Moore & Laudon, 1943
- Superfamily ALLAGECRINOIDEA
- Carpenter & Etheridge, 1881
- Family ALLAGECRINIDAE Carpenter & Etheridge, 1881

Kallimorphocrinus Weller, 1930

TYPE SPECIES

K. astrus typicum (= *K. astrus astrus*) Weller, 1930 from the Late Carboniferous Perth Limestone, Indiana; by original designation.

Kallimorphocrinus thaiensis sp.nov. (fig. 1A-I)

ETYMOLOGY.

From Thailand.

MATERIAL AND LOCALITY

Holotype UQF79668; paratypes UQF79669, 79670, silica replacements of thecae from a Permian unit, probably the Rat Buri Limestone, on Ko Muk.

DIAGNOSIS

Radials gently rounded, tumid. Thecal outline rounded pentalobate in oral view.

DESCRIPTION

Theca bowl-shaped, higher than wide, greatest width just above midheight, incurved to radial summit, rounded pentalobate in oral view. Dorsal cup tumid, flat-based, bowl-shaped, finely pitted.

BB 2 or 3, sutures obscured by silicification, forming lower 1/3 of cup height in lateral view, RR 5, approximately twice as long as wide, narrower at base than radial summit, convex horizontally and longitudinally, prominently rounded tumid at 3/4 length, subequal in size, becoming wider with increasing facets. Radial summit horizontal, 1-3 facets per radial. Facets with well developed transverse ridge; muscle field in moderately deep depression sloping inward to ambulacral canal. Anal facet small, equidimensional, on left shoulder of C radial. OO 5, well elevated, slightly inset on radial summit, forming a quarter thecal height, dart-shaped, shaft sides vertical, oral surface with two faint ridges parallel to sides, extending nearly to centre of circle. Posterior oral largest, separating BC and DE orals, probably bearing hydropore or madreporite. Proximal columnal circular transversely, much wider than high.

MEASUREMENTS OF HOLOTYPE (mm)

Thecal height, 3.1; maximum width, 2.6; height BB circle, 0.9; radial length 1.6, width, 1.4; height OO circle 0.7; proximal columnal diameter 1.3, height 0.2.

REMARKS

The description is based on the holotype, a specimen with 9 arm facets, 2 on A and B radials, 1 each on the C and E radials, and 3 on the D radial, and the paratype, a partial theca lacking the basal circle and adjacent basal ends of the radials. The paratype bears one arm facet on each radial and the A facet appears to have the initial stage of a second facet developing on the right side. Both specimens fit the generic definition as revised by Lane & Sevastopulo, 1982.

Kallimorphocrinus thaiensis is distinguished by the rounded protuberance of the radials being greatest at 1/2 thecal height. The Early Carbonif-

erous, *K. astrus* and *K. piasaensis*, also have their greatest protuberance below the radial facet but their protuberance is much sharper making their thecae more pointed pentalobate in lateral and oral views. The only other Permian species, *K. eaglei* (Strimple, 1966), from Oklahoma and Nevada has exceedingly bulbous radials and much lower basals.

An aberrant specimen with four orals is assigned to *K. thaiensis*. It has no arm facet on the A radial and the EA and AB orals are fused. There are two arm facets each on the B and D radials, and one each on the C and E radials. The BC oral is not preserved but facets for its articulation are visible on the specimen. The A radial is narrower than the other radials and narrowest at the top where it abuts the abnormal oral. The orals are larger and higher than those of the types.

Silicification has obliterated details of ornament and oral and radial facets. All are judged to be immature as they retain the oral plates.

Kallimorphocrinus? sp.

(Fig. 1G-J)

MATERIAL AND LOCALITY

UQF79666, 79667, silica replacements of thecae associated with *K. thaiensis* from the Early Permian Rat Buri Limestone, Ko Muk.

DESCRIPTION

Theca truncate bowl-shaped, higher than wide in immature forms, wider than high in more mature forms, walls gently flared outward nearly to radial summit, widest just below radial summit. Dorsal cup rounded pentalobate in oral view, walls smooth.

BB circle fused, low, forming lower 1/4 of cup in immature forms, shallowly concave on circular facet for stem attachment, flaring upward from edge of stem facet. RR 5, longer than wide, narrowest at base, flaring gently outward nearly to facet, moderately convex transversely; convexity increasing distal of facet, becoming wider with increasing number of facets. Radial facets with transverse ridges, outer ligament pits and muscle fields on deep pit sloping inward, with one or more facets per radial in adults. Anal notch small, on left shoulder of C radial.

OO 5, forming rounded dome; individually approximately dart-shaped, widest medially; walls straight, vertical; oral surface with shallow central depression bordered by narrow U-shaped rim closed on aboral end.

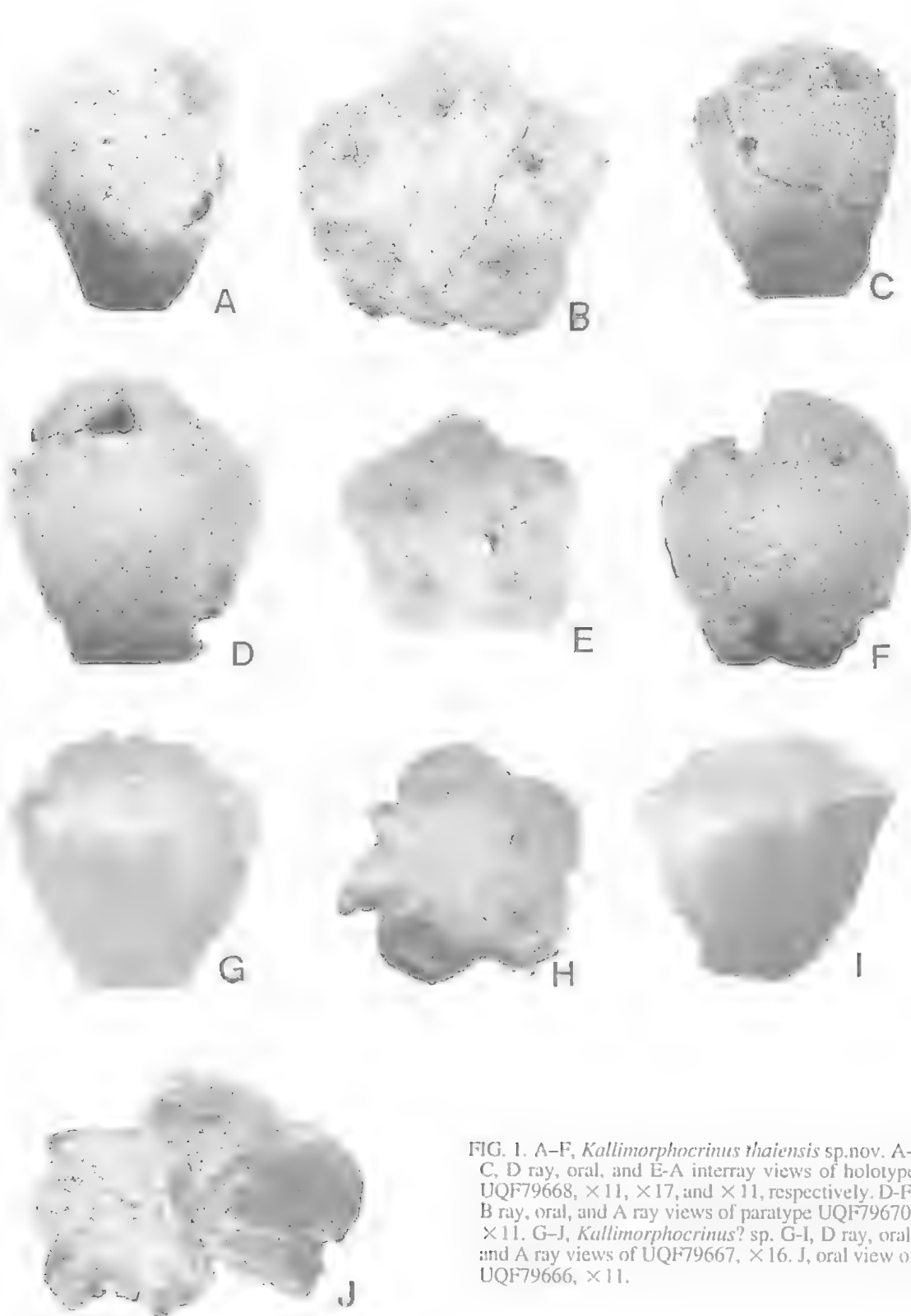


FIG. 1. A–F, *Kallimorphocrinus thaiensis* sp. nov. A–C, D ray, oral, and E–A interray views of holotype UQF79668, $\times 11$, $\times 17$, and $\times 11$, respectively. D–F, B ray, oral, and A ray views of paratype UQF79670, $\times 11$. G–J, *Kallimorphocrinus?* sp. G–I, D ray, oral, and A ray views of UQF79667, $\times 16$. J, oral view of UQF79666, $\times 11$.

MEASUREMENTS (mm)

	U Q F 79666	U Q F 79667
Height of theca	2.0	3.4*
Max. width of theca and cup	2.0	4.5
Height of dorsal cup	1.7	3.3*
Height of RR	1.3 (A)	3.1 (D)
Width of RR	1.0 (A)	1.8 (D)
Height of BB circlet	0.5	—
Height of OO circlet	0.3	0.1
Diameter of the stem facet	0.8	—

* estimated

REMARKS

The description is based on an immature five-armed theca lacking a small part of the outer wall of the C radial and a larger partial theca lacking virtually all the A radial, most of the B radial, and subjacent part of the basal circlet. This second specimen has one arm facet on the E radial, two on the D radial, one, two or three on the C radial, and at least one on the B radial. Silicification has obliterated some details of the oral plates and radial facet.

Doubts about generic assignment stem from two features. The anal notch could be a result of silicification on the smaller specimen and actually be an arm facet on the larger specimen. Secondly the radials closely resemble those of *Wrightocrinus jakovlevi*, to which this species could be related.

Kallimorphocrinus, as redefined by Lane & Sevastopulo, 1982, has up to 14 arms with only one arm in each of the C and E rays, an anal series, and loss of the orals in adults. Moore (1940) proposed *Wrightocrinus* as an allagecrinid with or without an anal series distinguished by the single arm on each of the B and E radials in adults. He designated *Allagecrinus jakovlevi* Wanner, 1929 as type. Wanner (1929) reported 125 specimens of *A. jakovlevi* and analysed 71 specimens as having 1 arm in each of the B and E rays with one exception having 2 arms in the B ray. Marez-Oyens (1940) reported an additional 199 specimens of *A. jakovlevi* with only 12 specimens having 2 (10 specimens), 3 (one specimen), or 4 (one specimen) arm facets on the B radial. It is possible that most of these exceptions are incorrectly identified and are actually kallimorphocrinids or other allagecrinids as they only have one arm facet on the C and E radials with one exception with two on the C radial.

The number of arms in each ray in adult microcrinoids may be generically diagnostic of some

allagecrinids (Moore, 1940; Moore & Strimple in Moore & Teichert, 1978). For example, *Wrightocrinus* normally has only one arm in each of the B and E rays, whereas *Kallimorphocrinus* has one arm in each of the C and E rays, and both genera have more than one arm in each of the other rays. The radials of the two specimens assigned to *Kallimorphocrinus*? sp. are very similar in shape to those of *Wrightocrinus jakovlevi* (Wanner, 1929) a Permian form from Timor. If there were no question about the number of facets on the B and C radials in the larger specimen we would assign the specimens unquestioned to either *Wrightocrinus* or *Kallimorphocrinus*.

The only other species, previously assigned to *Wrightocrinus* is *Allagecrinus biplex* Wright, 1932 (designated genotype of *Thaminocrinus* Strimple & Watkins, 1969), a Viscan form from Scotland with an anal series. Moore (1940) considered the lack of an anal series in the Permian species to be an advanced evolutionary feature for the genus. Neither Wanner (1929) nor Marez-Oyens (1940) recognised specimens of *A. jakovlevi* with less than 9 arms, however, they both recognised specimens of *A. quinquebrachiatus* Wanner, 1929, a form with 5 arms and no anal series and a cup shape, radial form and oral configuration like that of *A. jakovlevi* but approximately one half the size. Strimple (1966) proposed *Metallagecrinus* designating *A. quinquebrachiatus* as type. If *A. quinquebrachiatus* is the immature form of *W. jakovlevi*, as we believe, then *Metallagecrinus* is a junior synonym of *Wrightocrinus*.

Strimple (1966) assigned an additional 11 species to *Metallagecrinus* because they all lacked an anal series, retained the oral circlet, and had one arm per ray. Strimple & Sevastopulo (1982) reconsidered these assignments and suggested *M. multibrachiatus* (Yakovlev, 1927), *M. dux* (Wanner, 1930) and *M. inflatus* (Wanner, 1929) should be excluded because they differ in several respects from the type. We agree with this assessment and would transfer all other species [*M. acutus* (Wanner, 1929), *M. excavatus* (Wanner, 1929), *M. indoaustralicus* (Wanner, 1916), *M. quinquelobus* (Wanner, 1929), *M. procerus* (Wanner, 1929), *M. ornatus* (Wanner, 1929), *M. uralensis* (Yakovlev, 1927) and *M. uralensis nodocarinatus* (Yakovlev, 1927) as well as *M. palermoensis* Strimple & Sevastopulo, 1982 to *Litocrinus* Lane & Sevastopulo, 1982.

Order CLADIDA Moore & Landon, 1943
 Suborder POTERIOCRININA Jaekel, 1918
 Superfamily SCYTALOCRINOIDEA
 Moore & Laudon, 1943

Family and Genus uncertain

MATERIAL

One partly silicified dorsal cup, UQF79665, from acid residue of loose boulder of Rat Buri Limestone from the southeast part of small bay; Ban Hat Yao, on the northern end of Ko Yao Noi, southern Thailand.

REMARKS

This cup is 5.8mm wide, 3.4mm high, cone-shaped, with truncated base, steeply outflared plenary radial facets, with a single small anal in a notch shared by the C and D radials. Infrabasals small, slightly upflared. Ornament destroyed by silicification if present; stem facet round. Anal sac and arms unknown.

Advanced features present on the cup are the plenary facets and anal plate nearly out of the cup. A primitive feature retained is the conical shape. The specimen is questionably assigned to the scytalocrinoids because of its shape, radial facets, and number and position of the anal.

The specimen is not well enough preserved to be designated a type or effectively illustrated. It is mentioned because it adds to the generic diversity in the Permian of Thailand.

Superfamily DECAODOCRINOIDEA Bather,
 1890

Family CLATHROCRINIDAE Strimple &
 Moore, 1971

Clathrocrinid gen. et sp. nov.
 (Fig. 2 O,P)

MATERIAL AND LOCALITY

One crown, USNM450329, from acid residue of the Rat Buri Limestone, locality USNM9271, northwest side of Ko Muk, NW of Kan Tang (Grant, 1976).

DESCRIPTION

Crown small, elongate, subcylindrical, with arm girdle at top of primibrachials, 10 arms slender with offset brachials in zig-zag pattern. Cup crushed, medium bowl; walls outflaring, gently convex; base invaginated; sutures flush; radial notches obvious; ornament lacking. IBB not visible in lateral view. BB 5, slightly longer than wide, gently convex transversely, strongly convex proximally, gently convex distally, proximal

end forming base of cup. RR 5, wider than long, gently convex transversely and longitudinally; facet angustary, lacking prong-like internal extensions on lateral ends of upper surface; small gape with primibrachials at facet. Single anal relatively large, longer than wide, with proximal third below radial summit, sitting on top of truncated laterally symmetrical CD basal, with distal two-thirds incurved above radial summit, adjoined distally by two tube plates. IBrr one per ray, axillary, longer than wide, widest at base, laterally constricted in central three-fourths, strongly convex transversely, gently concave longitudinally, bearing prominent slightly upward directed spine at distal end. IIBrr elongate, cuneate, twice as long as wide proximally, three times longer than wide distally, widest on distal end, strongly convex transversely, longitudinally straight becoming concave distally, bearing prominent slightly upward directed spine on distal end. Pinnules large, could be considered ramules, elongate, strongly convex transversely, alternate on sides of arm, one per brachial on distal end of brachial.

MEASUREMENTS (mm)

Crown length 31.6 (incomplete), width 10.6; cup height 5.8, width 4.2 (estimated); BC basal length 3.6, width 3.5; E radial length 4.2, width 5.8; anal length 3.8, width 3.2; IBrr length 4.1, width 3.8; IIBrr length 5.8, width 2.8; IIBrr5 length 4.6, width 1.7.

REMARKS

No name is given to this distinctive specimen because the cup is crushed. Infrabasals are not preserved; the BD, CD and DE basals and C, D and E radials are preserved.

Classification is based on arm structure. The angustary radial facets, elongate brachials, pinnules that are essentially ramules, zig-zag pattern of the brachials, and spine on the distal end of the brachials all have affinity with the Clathrocrinidae. Unlike *Clathrocrinus* only one anal occurs within the radial summit, indicating an advanced condition, and the zig-zag pattern of the brachials is not as widely spreading. We consider this specimen to have evolved from a clathrocrinid ancestor in Early Permian times. Range of the family is extended into the Permian and its distribution, previously confined to North America, is extended to Southeast Asia.

Superfamily ERISOCRINOIDEA Wachsmuth
& Springer, 1886

Family GRAPHIOCRINIDAE Wachsmuth &
Springer, 1886

Contocrinus Knapp, 1969

TYPE SPECIES

Graphiocrinus stantonensis Strimple, 1939
from the Upper Carboniferous Wann Formation,
Oklahoma, by original designation.

Contocrinus andamanensis sp. nov.
(Fig. 2E-H)

ETYMOLOGY

For the Andaman Sea.

MATERIAL

Holotype USNM450326; paratype USNM450325,
Rat Buri Limestone, locality USNM9271, NW side of
Ko Muk, Thailand.

DIAGNOSIS

Small, with a shallow arm girdle, large elongate posterior basal, and anal distally adjoined by two tube plates.

DESCRIPTION

Crown elongate, slender, with slight arm girdle at base of secundibrachials, 10(?) arms. Cup medium bowl-shaped, widest slightly below radial summit, with moderate basal invagination; sutures between basals slightly impressed, sutures between radials deeply impressed; apical pits at top of basals and base of radials; granular to vermiform ornamentation. IBB 5, small, slender, strongly tapering, downflaring, not visible in lateral view, covered by proximal columnal. BB 5, outflaring, strongly convex longitudinally and transversely, slightly wider than long, proximally forming base of cup; posterior basal larger, more elongate. RR 5, slightly outflaring, wider than long, strongly tumid. Radial facets plenary, sloping outward, with moderate gape; outer ligament area wide, with pit; transverse ridge full width of facet. Anal slightly longer than wide, proximally adjoining truncated transversely symmetrical CD basal, distal end projecting slightly above radial summit, followed by two tube plates. IBBr one per ray, axillary, medially constricted, strongly convex transversely, gently concave longitudinally, slightly wider proximally than distally. IIBr slightly longer than wide, slightly cuneate, strongly convex transversely, weakly convex

longitudinally; sutures slightly impressed. Proximal columnals heteromorphic, transversely round, latus convex, symplexy articulation; lumen not preserved.

MEASUREMENTS (mm).

	U S N M 450325	U S N M 450326
Crown length (incomplete)	14.0	15.0
Cup height	2.0	3.4
Cup width (through A-CD)	8.0	7.7
Diameter IBB circlet		0.9
AB basal length	1.8	2.4
AB basal width	1.9	2.8
A radial length	1.7	2.4
A radial width	2.8	3.2
IBR1 length	2.9	4.5
IBR2 width	2.8	3.7
IIBR1 length	1.9	2.5
IIBR1 width	1.7	2.2
IIBR5 length	1.2	1.4
IIBR5 width	1.6	1.9
Anal length	1.8	1.6
Anal width	1.4	1.5
Diameter proximal columnal	1.5	1.3

REMARKS

There are probably 10 arms. The D and E rays are not preserved on the paratype and the A, B and E rays are not preserved on the holotype. All preserved rays bear 2 arms. Pinnules are not preserved on either specimen but articular facets for the pinnules are poorly preserved on the distal outer corner of some of the distal secundibrachials. Noditaxis patterns are not well developed on the proximal pluricolumnal segment, but variable thicknesses of the 6 columnals suggest a simple heteromorphic Type 1 pattern of Webster (1974). Ornamentation is more finely granular on the holotype than the paratype.

These specimens are transitional between the graphiocrinids and apographiocrinids. The arm girdle and two tube plates adjoining the anal plate relate the specimens to the apographiocrinids. However, plenary radial facets and lack of prong-like extensions on the radials between the facets show affinity to the graphiocrinids. We consider the plenary radial facets to be of greater importance in classification than the number of tube plates adjoining the anal plate.

Contocrinus andamanensis has less tumid cup plates and a longer posterior basal than the most similar *C. scopulus* (Lane & Webster, 1966). Both

species are smaller than Pennsylvanian species; because both are based on few specimens, it is not known if they are mature or not.

This is the first report of *Contocrinus* outside North America, although graphiocrinids, i.e. *Permiocrinus* Wanner, 1949 is known from Timor. Most Timor species initially assigned or transferred to *Graphiocrinus* by Wanner, 1949, have been assigned to other families of advanced potentiocrinids (Webster, 1987, among others).

Superfamily APOGRAPHIOCRINOIDEA
Moore & Laudon, 1943

Family APOGRAPHIOCRINIDAE Moore &
Laudon, 1943

Apographiocrinus Moore & Plummer, 1940

TYPE SPECIES

A. typicalis Moore & Plummer, 1940 from the Pennsylvanian Plattsburg Limestone, Kansas, U.S.A., by original designation.

Apographiocrinus komukensis sp. nov.
(Fig. 2A–D)

ETYMOLOGY

From the island of Ko Muk.

MATERIAL

Holotype USNM450328 and paratype USNM450327 from acid residues of Rat Buri Lst at locality USNM9271, NW side of Ko Muk.

DIAGNOSIS

High cup, with less tumid plates, ornament variable, finely granular to vermiform.

DESCRIPTION

Cup medium bowl-shaped, nearly twice as wide as high; walls gently convex, outflared; base with moderately deep invagination; sutures weakly impressed; apical pits shallow; ornament very fine and granular. IBB 5, small, dart-shaped, downflaring, not visible in lateral view. BB 5, slightly wider than long, gently convex transversely and longitudinally, proximal end forms base of cup and edge of basal invagination. RR 5, wider than long, gently convex longitudinally, strongly convex transversely; facets angustary, sloping outward; internally extending prong-like ridges separating facets; well developed radial notches in lateral view. Anal slightly longer than wide, proximal end adjoins truncated laterally symmetrical CD-basal, distal third extends above

radial summit, facets for two adjoining tube plates distally. IBrr one per ray, slightly longer than wide, constricted medially, transversely convex, longitudinally concave; axillary, isotomous branching. Stem impression round.

MEASUREMENTS (mm)

	USNM 450328	USNM 450327
Crown height	4.2	3.0*
Cup width	7.6	6.0
Diameter IBB circlet	2.0	1.5
AB basal length	2.5	2.0
AB basal width	2.9	2.4
A radial length	2.4	2.0
A radial width	4.0	3.4
Anal length	2.1	—
Anal width	1.6	—
IBR1 length	—	2.9*
IBR1 width	—	2.7

*estimated

REMARKS

The paratype has more tumid cup plates, some vermiform ornamentation, more impressed sutures, and a lower, more outflaring bowl configuration than the holotype. Although possibly distinct species we consider them one on available material. Angustary radial facets, prong-like projections between radial facets, and facets for two tube plates distal to the anal relate these forms to *Apographiocrinus*.

Three species of *Apographiocrinus*, *A. pumilus*, *A. quinquelobus*, and *A. rugosus*, although initially assigned to other genera, were reported from Permian strata of Timor by Wanner, 1916. All three species have much coarser ornament, ornament of a different type, or much more tumid basals and radials than *A. komukensis*. Late Carboniferous species of *Apographiocrinus* known from North America have less tumid cup plates, are much larger, and have more outflared cup walls than *A. komukensis*.

Apographiocrinus? sp. nov.
(Fig. 2L–N)

MATERIAL AND LOCALITY

One partial crown, UTGD124566 from the basal part of the Rat Buri Limestone from Ko Phi Phi, an island northwest of Kan Tang, recovered by Clive Burrett. Sample No KP(B).

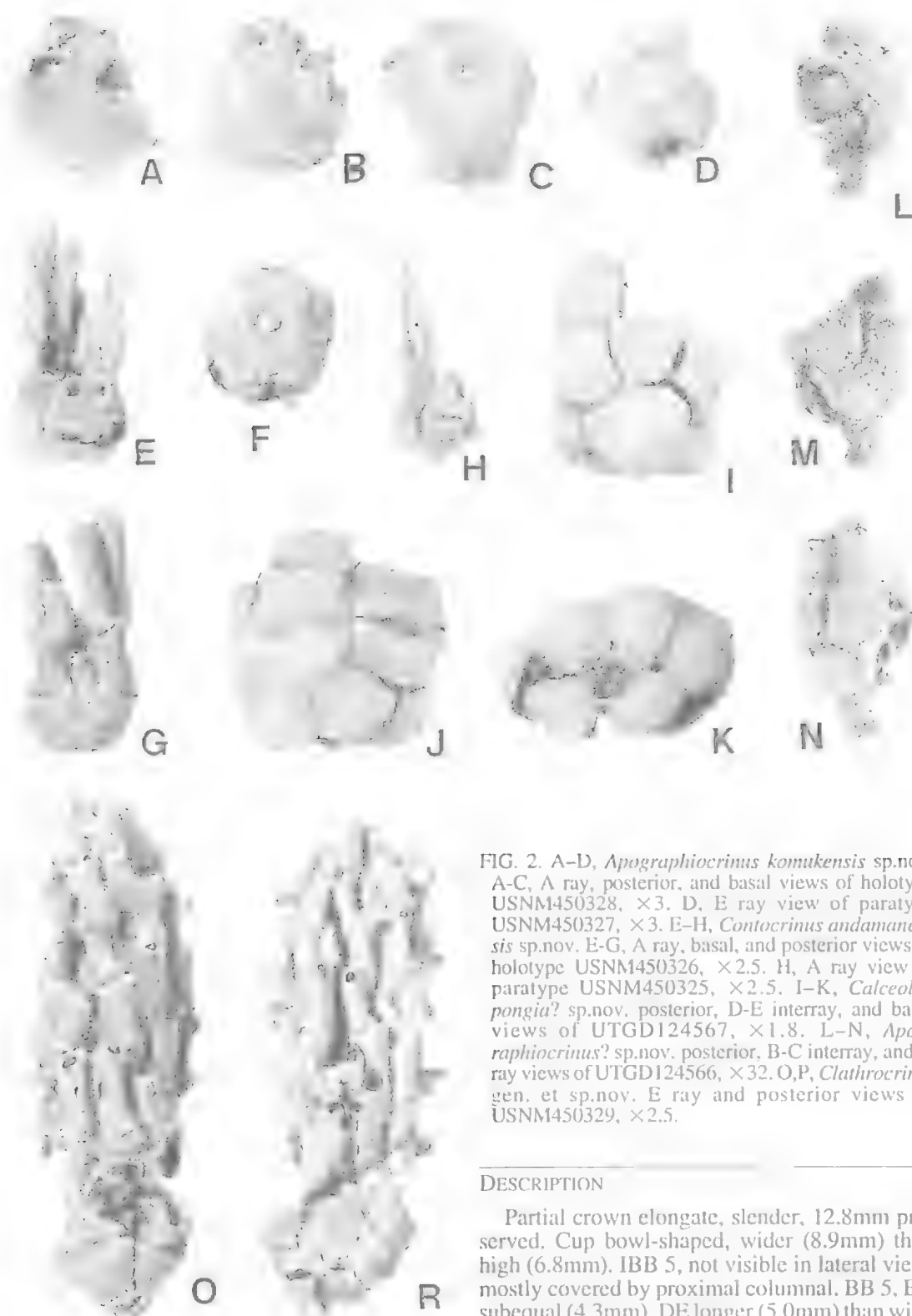


FIG. 2. A-D, *Apographiocrinus komukensis* sp.nov. A-C, A ray, posterior, and basal views of holotype USNM450328, $\times 3$. D, E ray view of paratype USNM450327, $\times 3$. E-H, *Contocrinus andamanensis* sp.nov. E-G, A ray, basal, and posterior views of holotype USNM450326, $\times 2.5$. H, A ray view of paratype USNM450325, $\times 2.5$. I-K, *Calceolispongia?* sp.nov. posterior, D-E interray, and basal views of UTGD124567, $\times 1.8$. L-N, *Apographiocrinus?* sp.nov. posterior, B-C interray, and A ray views of UTGD124566, $\times 32$. O,P, *Clathrocrinid* gen. et sp.nov. E ray and posterior views of USNM450329, $\times 2.5$.

DESCRIPTION

Partial crown elongate, slender, 12.8mm preserved. Cup bowl-shaped, wider (8.9mm) than high (6.8mm). IBB 5, not visible in lateral view, mostly covered by proximal columnal. BB 5. EA subequal (4.3mm), DE longer (5.0mm) than wide

(4.8mm), convex proximally forming basal plane, gently convex and subvertical distally. Posterior basal heptagonal, truncated distally for reception of anal. RR 5, A radial wider (4.8mm) than long (3.5mm), moderately convex transversely, gently convex longitudinally, subvertical to slightly incurved distally, lateral sutures impressed. Radial facets peneplenary, sloping gently outward, low lateral prongs extending internally as lateral ridges with adjoining radials. Single anal longer (2.9mm) than wide (2.1mm), gently convex transversely and longitudinally, proximal 3/4 below radial summit, adjoins 2 tube plates distally.

IBrr one per ray, axillary, longer (6.5mm) than wide (4.5mm) widest at base, longitudinally convex-concave, transversely convex, constricted below distal facets, unequal in length, ?A ray IBr longest. Proximal columnals heteromorphic, transversely rounded, latus gently convex, lumen ?pentalobate.

REMARKS

The specimen is silicified and slightly distorted basally. Parts of B radial and AB through CD basals not preserved. Only A and E IBr complete. C & E IBr partly preserved. The infrabasal circlet is not visible but internal walls of etched basals show two facets for attachment to infrabasals. There were probably 5 small infrabasals down-flared or subhorizontal.

The arms branch isotomously on the E and A primibrachs, suggesting 10 arms if the same branching pattern occurred in all rays.

The specimen is referred to the Apographeocrinidae because it has peneplenary radial facets, lateral prongs on the radial facets, and 2 tube plates distal to the single anal. The cup is more elongate than in the rest of the family, indicating a less advanced form than might be expected in a Permian member. Constriction in the distal part of the primibrachs suggests development of an arm girdle. It is left in open nomenclature in hope of future recovery of additional specimens.

Cymbiocrinus? sp. nov.
(Fig. 2I-K)

MATERIAL AND LOCALITY

Partial crown, UTGD124567, found by Clive Burrett in the upper Phuket Group on Ko Phi Phi. It occurs in a unit with Early Permian brachiopods considered to indicate a temperate climate (Waterhouse, 1982).

DESCRIPTION

Partial crown crushed subparallel to anterior-posterior plane of symmetry. Cup moderate bowl-shaped, with shallow to moderate basal invagination; plates bulbous, not ornamented. IBB not preserved. BB 5, strongly convex in all directions, subequal length (8.4mm) and width (8.1mm), forming basal plane, hexagonal except heptagonal posterior basal truncated for anal plate. RR 5, half again wider (10mm) than long (6.3mm), convex longitudinally and transversely. Radial facets plenary.

Single large anal, essentially below radial summit, gently convex longitudinally and transversely, longer (4.7mm) than wide (4.6mm). IBrr 2 in B ray, wider (9.7mm) than long (5.2mm) gently convex longitudinally and transversely, IBr2 axillary. C ray IBr larger, 10.2mm wide, 5.8mm long, non-axillary. Additional brachials and stem not preserved.

REMARKS

Specimen replaced by hydrous iron oxides, B radial lost, some loss by solution of plates adjacent to B radial. Radial facets well developed and sloping inward but solution has destroyed details of exposed surfaces. Infrabasals lost, small, probably 5 and down flared or subhorizontal, mostly covered by proximal columnals. Pluricolumnal segments in the matrix block are transversely rounded but not attached to the cup. It is not certain that they were part of the original animal but it seems likely.

The bulbous basals and large radianal suggest relationship with the calceolispongiids. However, branching on the second primibrach is unknown in the calceolispongiids but is typical of *Cymbiocrinus* which has a single anal. We consider the calceolispongiids to have evolved from the Cymbiocrinids adapting to cooler water elastic dominated environments of the Permian of Australia. The specimen is left in open nomenclature in hope of a future discovery of a better specimen to serve as holotype.

ACKNOWLEDGEMENTS

Our appreciation is extended to Richard E. Grant, Clive Burrett, and Bruce Waterhouse for the loan of material. Frances G. Stehli provided funding and aided in the collection of the material deposited in the USNM.

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LATE TRIASSIC HOMOPTEROUS NYMPH FROM DINMORE, IPSWICH BASIN. *Memoirs of the Queensland Museum* 33(1): 360. 1993:- This well-preserved homopterous nymph was collected by Mr Robert Knezour from plant fossil-rich mudstone underneath powerlines in a quarry (Queensland Museum [QM] L471) at the end of Roberts St, Dinmore in the Ipswich Basin (27°31'S, 152°51'E). The sediments belong to the Blackstone Formation of the Ipswich Coal Measures. Palynological data suggest a Late Triassic (Carnian) age (deJersey, 1970). Details of stratigraphy and age were given by Rozefelds & Sobbe (1987) who noted other insects (Blattodea, Hemiptera and Coleoptera) in association with a typical *Dicroidium* macroflora.

Order HEMIPTERA

Suborder HOMOPTERA

Superfamily UNCERTAIN

The head with the rostrum arising from the front near the rear of the head suggests an homopterous form but its relationships are uncertain because comparable nymphs are extremely rare in the fossil record. Of the several homopterous nymphs known (Riek, 1974 and references therein) none are similar to the new form being mainly Sternorrhyncha whereas this fossil is more like Auchenorrhyncha nymphs (Carpenter, [1992] did not report any nymphs in families referable to the Auchenorrhyncha). Because several critical features are unclear on the fossil, comparison with nymphs of Recent forms can only be superficial and therefore inconclusive. However, it does suggest similarity to Fulgoroidea. The excessively long rostrum, patches of sensory abdominal tubercles, and long coxae based well away from the midline are known in modern Fulgoridae. However, unlike the fossil described here, coxae of the third fulgorid leg are fixed in the sternite and the free part of the leg begins at the tibia. Familial assignment must remain open.

***Knezouria* gen. nov.**

Type species. Knezouria unicus sp. nov.

Remarks. Although it is possible that this nymph belongs to a named fossil species, there is no way of determining its morphogenetic development and no way of relating it to an adult. Therefore, a separate binomial name is justified for a fossil that cannot be assigned to an existing taxon and that is likely to be referred to often.

***Knezouria unicus* sp. nov. (Fig. 1)**

Etymology. Latin *unicus*, sole, one only.

Material. Holotype QMF18850a,b (part & counterpart), ventral surface only.

Description. Nymph with rudimentary wings (most obvious posterolaterally on thorax); 13mm long, 7mm wide, abdomen half length of animal. Frons large, diamond-shaped, with subtle transverse and longitudinal ridges meeting at midpoint; rostrum very slender, extending beyond the posterior margin of the abdomen (preserved as an indistinct ridge curving off the midline along the thorax then crossing the midline near abdominal midlength); posterior of head indistinct.

Legs with long, stout, oblique coxae, based away from midline and running to midline; femora strong, similar, running obliquely to margin; tibia long, slender, may have fine



Fig. 1. *Knezouria unicus* gen. et sp. nov. holotype, part and counterpart of ventral surface. A, B.

spines on inner edge; tarsi 0.3 length of tibia, gently curved; pretarsus with two claws.

Abdomen inverted beehive shape, 8 segments clearly evident, with distinct, narrow, median longitudinal ridge, with paired areas of small tubercles on each segment (each one associated with a sensory hair, by analogy with modern Homoptera). Terminal (8th) segment with anal and genital structures in median line well forward of margin, in form of two pairs of lobes directed posteriorly, each pair forming an indistinct U-shaped structure.

Acknowledgements

I am grateful to Mr Robert Knezour for donating the specimen and allowing me to describe it.

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Peter A. Jell, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 22 December, 1992.

SURVEY OF THE VERTEBRATE FAUNA OF THE DOTSWOOD AREA, NORTH QUEENSLAND

STEVE WILLIAMS, RICHARD PEARSON & SCOTT BURNETT

Williams, S., Pearson, R. & Burnett, S. 1993 06 30: Survey of the vertebrate fauna of the Dotswood area, north Queensland. *Memoirs of the Queensland Museum* 33(1): 361-378. Brisbane. ISSN 0079-8835.

The results of a survey of mammals, birds, reptiles, amphibians and fish of the Dotswood area west of Townsville are presented. Habitats included in the survey were woodland, open forest, tall open forest, closed forest (rainforest), riparian forest and rocky outcrops. A total of 297 species of vertebrates were observed using a variety of survey techniques including live trapping, pit trapping, observational transects, mist netting and spotlighting. Exact locations of observations and indices of relative abundance of each species are included.
☐ Survey, vertebrate, mountain, Dotswood, north Queensland, Australia.

Steve Williams, Richard Pearson & Scott Burnett, Australian Centre for Tropical Freshwater Research, James Cook University of North Queensland, Queensland 4811, Australia; 15 November, 1993.

Fauna surveys, although mostly descriptive, are a basic necessity in the understanding of the ecology of any area. This paper describes a broad survey of the vertebrates in a variety of habitats west of Townsville, undertaken to provide baseline information prior to the proposed development of military training facilities. Despite its proximity to and accessibility from Townsville, the survey area, which includes Dotswood Station, Star Station, High Range Training Area and sections of the Bluewater Range, had never been the subject of any intense biological studies. Consequently, very little published biological information exists for the area. Not only is information on the area poorly represented in the literature, but the wet-dry tropical environment of north Queensland which typifies much of the Dotswood and High Range areas is very poorly understood. This reflects the concentration of Australian zoological and ecological research effort in southern regions and the tropical coastal zone in the past.

The study area is located within the Shire of Dalrymple to the south-west of Townsville (Fig. 1), with the north-eastern and eastern boundaries following the escarpments of the Paluma and Hervey's Ranges. The western boundary is to the west of the Star River and the southern boundary follows the boundary between Dotswood Station and Fanning River Station (Fig. 2).

The total study area of about 2320km² comprises the following land tenures:

High Range Training Area (HRTA)	48,669ha
Dotswood Pastoral Lease (No. 44/3176).	155,000ha

Special Lease RAAF training area (N 44/45266) . .	27,300ha
Occupational License (No. 510)	907ha
Total study area approximately	232,000ha

The landscape descends from the escarpments and hills of Paluma and Hervey's Ranges (altitude c.800m) in the north and east to a complex of dissected plateaux and tablelands with steep slopes to the south, through to areas of low relief (altitude c.250m) in the south-west. The study area is drained by the Star River, Keelbottom Creek, Fanning River and the Reid River. Drainage direction is generally to the south, with all drainage systems except the Reid River draining into the Burdekin River. The Reid River flows into the Haughton River.

The emphasis of the study was on recording the diversity of the vertebrate fauna in each of the major habitat types of the study area, with some regard to relative abundances. Sampling methods were therefore designed to record as many species of mammals, birds, reptiles, amphibians and fish as was possible. Additionally, literature on the study area was reviewed and a reasonably comprehensive species list of the area was compiled.

Additional sources of information included rare and threatened species lists from Queensland National Parks and Wildlife Service (QNPWS); endangered species list from ANZECC (Anon, 1991); assessments of status and lists of rare, endangered, vulnerable and poorly known vertebrates of Queensland, and location records of mammal, bird, reptiles and frogs from the Queensland Museum database (Ingram & Raven,



FIG 1. Map of north Queensland showing location of study area.

1991), the most up-to-date assessment of the status of vertebrates in Queensland; species records from the Wildlife Preservation Society of Queensland; Williams et. al., (1993); Ben Lomond (Hollingsworth, 1980); Brouwer & Garnett's (1990) annotated list of threatened birds of Australia; and a variety of personal communications with staff at James Cook University and the QNPWS.

LITERATURE REVIEW

BIRDS

Most bird records from the region are from the coastal plains and ranges. Lavery & Johnson (1968) provided a list of observations from the Townsville area, from Mt Spec in the north to 'St Hellions' near Cape Cleveland in the south. This study identified 229 species from the area. Blakers et. al. (1984), which provided Australia-wide maps for all the Australian birds mapped in $1^{\circ} \times 1^{\circ}$ squares (19°S 146°E), recorded 256 spp. from the region encompassing the study area. Nix & Switzer (1991) gave locality and expected ranges of all vertebrates considered to be endemic to the wet tropical rainforest. Steve Garnett (pers. comm.) listed 365 species from the Townsville area and Hollingsworth (1980) listed 64 bird spe-

cies at the Ben Lomond mine on Dotswood. Queensland Museum specimen records are scanty, including only three species from the Dotswood area.

Due to the relative ease of observation and identification of birds, they feature strongly in the lists of amateur wildlife groups, such as, the Townsville Bird Banding Group, which has undertaken a long term study in tall open forest west of Paluma, and the Wildlife Preservation Society of Queensland, which provides bird lists in excursion reports from the Townsville area, including Bluewater and Hervey's Ranges and Fanning River. In addition, QNPWS provide bird lists for national parks of the area including Mt Spec and the Townsville Town Common. Where relevant, species recorded by these sources have been included in this report.

Ecological studies in the area are much scarcer than simple records of occurrence. Apparently no studies have been conducted within the study area itself or within equivalent open forest in the region. Keast et. al. (1985), however, bring together information on eucalypt forest birds, some of which may be applicable to this area (e.g. Keast, 1985; Recher, 1985).

Rainforest birds have received more attention in north Queensland. Kikkawa (1982) examined the community structure of rainforest birds in relation to rainforest physiognomy and Crome (1978) examined the feeding ecology of birds in lowland rainforest. Although these studies were conducted at lower altitudes than the study area their results should be applicable to rainforest on the Bluewater Range. However, while some studies have been conducted in comparable areas and may be applicable to the study area, information on habitat utilisation, particularly the role of wet refugial areas (i.e. riverine and vine thicket habitats, and responses to disturbance) is scanty. Stocker & Irvine (1983) and Crome & Moore (1990) have discussed the ecological role of the Southern Cassowary in dispersal of rainforest seeds.

MAMMALS

Winter et. al. (1984) provided a list of 16 rainforest mammal species either recorded or expected from the Bluewater region which is partly contained within the RAAF training area. Lavery & Johnson (1968) gave a list of 71 mammals from the coastal plains and ranges of the Townsville area. No equivalent published lists are available from the drier habitats that typify most of the study area, although Hollingsworth (1980) listed

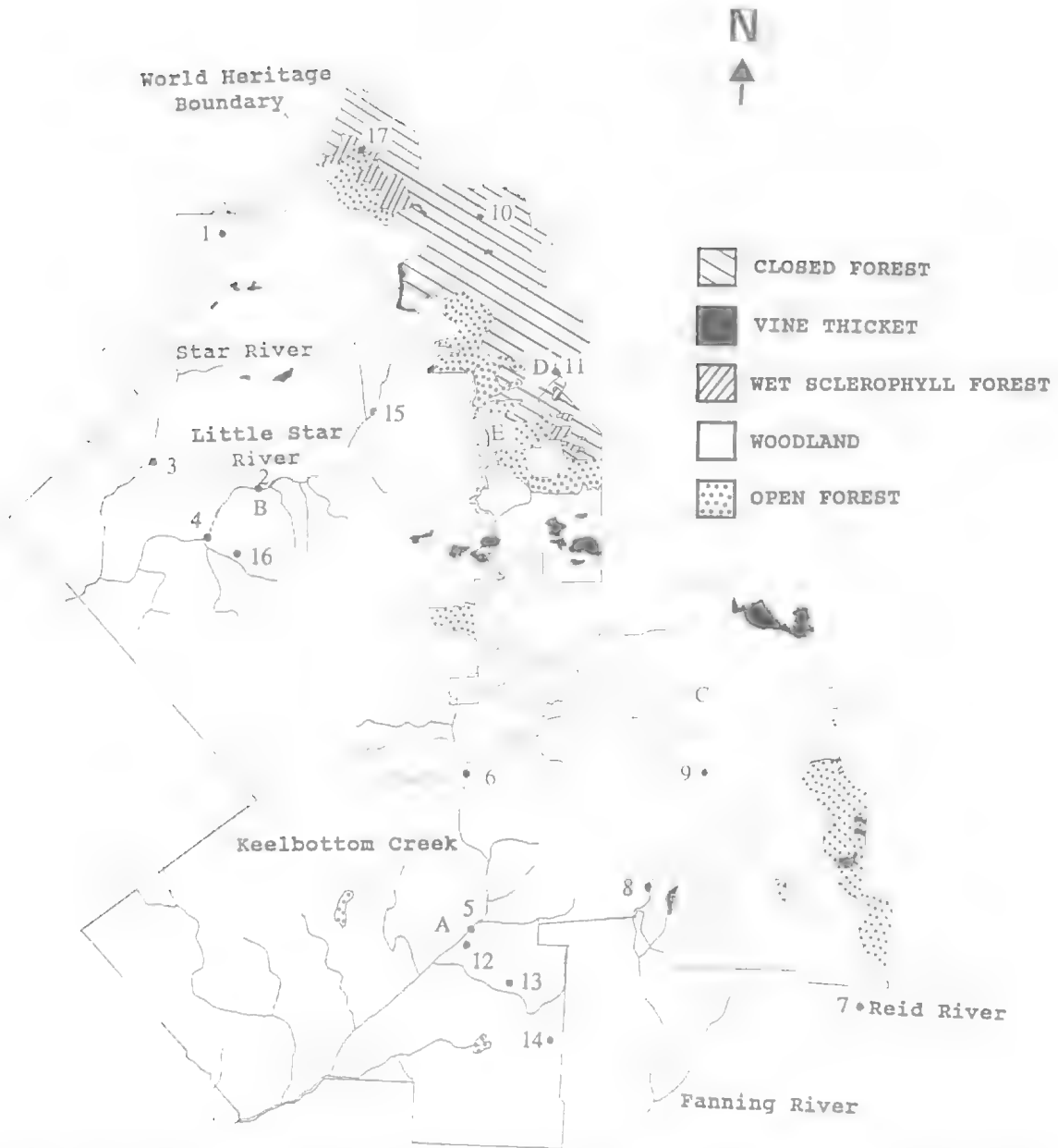


FIG 2. Map of the study area showing site locations and major fauna habitat types and streams (riparian habitat). Major vegetation boundaries after Power & Jackes (1992).

13 mammal species, five of which were introduced, at the Ben Lomond mine site on Dotswood. A QNPWS survey of the Dalrymple Shire covers an area of comparable habitats to the west of the study area, but the results of this survey were not available.

Queensland Museum records provide a list of

nine species from Hervey's Range and areas on Dotswood Station while QNPWS provide lists for Mt Spec National Park and Townsville Town Common Environmental Park, which may be applicable to wetter parts of the Dotswood area. At Mt Spec, near Paluma, Williams (1990) examined the relationships between mammal commu-

nities and vegetation in wet forests similar to those in the study area at Bluewater State Forest.

REPTILES

Like mammals, reptiles are mostly cryptic and there is considerable confusion surrounding the taxonomy of many groups. Therefore it is not surprising that, until recently, very little had been published on the distribution and population and community ecology in this group (Strahan, 1985). However, Greer (1989) provided summaries of information on species biology for the lizards.

Queensland Museum records list 27 species of reptiles from the Bluewater/Hervey's Range/Dotswood area and Hollingsworth (1980) listed 23 species at Ben Lomond mine on Dotswood. Both these numbers are probably poor reflections of the true reptile diversity of the area as gleaned from distribution maps (Cogger, 1992; Wilson & Knowles, 1988).

The recent upsurge in interest in the wet tropics has led to increased collecting activity in the area. As a result, the distribution and status of rainforest species is generally better understood than for the species of the drier forest and woodland to the west (e.g. Nix and Switzer 1991). However, for the vast majority of reptiles from this area, and indeed from most of Australia, very little is known of community ecology or of specific habitat requirements (e.g. Wilson & Knowles 1988). The responses of species and communities to natural and human disturbances is unknown.

AMPHIBIANS

A considerable increase in interest in frog ecology and taxonomy has happened in the past 20 years (McDonald, 1992; Covacevich & McDonald, 1991; Ingram & Raven, 1991). This increase is reflected in an increase in the number of taxonomic studies (e.g. Czechura et. al., 1987; Liem 1974; Zweifel 1985) and, coupled with recent interest in the wet tropics, has led to a reasonable understanding of rainforest frog distribution patterns. McDonald (1992) provided a list of 23 rainforest species, 21 of which were endemic to tropical rainforest in north Queensland. Of this list, five, all with conservation prognoses of very good or excellent, are recorded from the Bluewater Range. A further five species are recorded on Queensland Museum lists from the drier areas of the study area and six species are listed from the Ben Lomond mine site on Dotswood Station (Hollingsworth, 1980).

Tyler (1979) described our knowledge of Australian frogs as abysmal and, although they have

received much more attention since that time, our understanding of population and community ecology is still at a basic level, especially in the wet/dry tropics. He listed potential impacts of humans on frogs including deforestation, land drainage, introduction of predators (including aquatic predators), and siltation of water bodies. Some species have benefited through human activities including provision of water bodies in dry areas. Habitat utilisation, including, for example, the importance of wet refugial areas, is not known.

FISH

Published material on the aquatic biota of the region is scarce. Pearson (1991a) reviewed much of the available information and discussed some of the major research needs for the wet tropics forest area. There is some information produced by the QNPWS for the coastal wetlands near Townsville, mostly on the avifauna, and one or two publications on the limnology of the Ross River Dam (e.g. Finlayson & Gillies, 1982). However, these coastal wetlands are not comparable with the natural aquatic habitats in the study area. The ecology of the middle Burdekin River has been studied by a research team at James Cook University, but apart from a short report (Pearson, 1991b) this work remains unpublished. Current studies on fish communities in the Star and Fanning Rivers include sites within the study area, but the work is incomplete and unpublished (B. Pusey, pers. comm.).

Studies of streams in the drier areas comparable with the study area are limited. They include the work on fish communities in the Black River (Beumer, 1980), on catfish populations in Campus Creek, an intermittent stream on James Cook University campus (Orr & Milward, 1984), and on the invertebrate communities of Campus Creek (Smith & Pearson, 1984, 1987).

It is clear, therefore, that the wet/dry forests and woodlands to the west of the wet, coastal ranges have been largely ignored in comparison to the rainforests. Additionally Ridpath (1985) noted that far less research has been conducted into ecological processes of the wet/dry tropics than in temperate or arid regions of Australia. He also pointed out the dangers in trying to apply models from these areas to the wet/dry tropics.

SAMPLING SITES

TERRESTRIAL

Site selection was aimed at replicated sampling of the maximum number of habitat types possible

within the constraints of time, equipment and personnel. The following broad habitat types were identified within the study area from the vegetation map by Power & Jackes (1992) (Fig. 2) and their detailed vegetation descriptions:

CF: closed forest;

TOF: tall open forest or 'wet sclerophyll forest';

OF: open forest;

W: woodland;

R: riverine (riparian) forest;

RK: rocky outcrops;

SW: swamps and other water bodies;

G: grasslands, mostly artificially cleared;

A pilot survey was used to ground-truth the habitat types and to select sampling sites within each broad vegetation type (Fig. 2). Within each of these sites, three or four different sub-sites were selected for intensive sampling. These sub-sites were chosen to maximise the diversity of habitats sampled within each broad vegetation type. The sites were (grid references refer to Australian 1:50 000 topographic maps, series R733):

SITE A: Woodland (W), vicinity of Dotswood homestead. This site is representative of the large areas of *Eucalyptus crebra* open woodland that cover most of the study area. Three sub-sites were: A1 - riparian vegetation along Keelbottom creek (19°37'S 146°19'E; grid ref. DU 247293); A2 - open woodland with grass understorey (19°36'S 146°17'E; grid ref. DU 227314); and A3 - open woodland with a shrub layer of *Acacia* sp. and grass understorey (19°35'S 146°15'E; grid ref. DU 216330).

SITE B: Woodland (W), between Star homestead and Ponto Hut. This second open woodland site was selected because this vegetation type covered a large proportion of the study area and the fauna might differ between the northern (site B) and southern (site A) areas. Three sub-sites were: B1 - low open *E. shirleyi* woodland with low shrubs along small dry gullies (grid ref. DU 151635); B2 - riparian vegetation (R) along the Little Star river and *E. platyphylla* woodland with dense grass layer (*Heteropogon* sp.) (19°18'S 146°12'E; grid ref. DU 149647); B3 - *E. crebra* open woodland with grassy (*Heteropogon* sp.) understorey (19°19'S 146°18'E; grid ref. DU 206645); B4 - mixed *Eucalyptus* open forest with sparse grass, predominantly *Themeda* sp.

SITE C: Open forest and woodland (OF and W) in the High Range training area. This area consists of denser vegetation than sites A and B with a greater tree diversity. The area is hilly with some rocky outcrops. Four sub-sites were: C1 - *Melaleuca* swamp with sedge and blady grass understorey (19°23'S 146°29'E; grid ref.

DU466554); C2 - riparian vegetation along Stake Creek (major tributary of the Fanning river) (19°27'S 146°30'E; grid ref. DU 480481); C3 - Rocky outcrop (19°27'S 146°30'E; grid ref. DU 402482); C4 - open eucalypt forest with grass (*Themeda triandra*) understorey (19°31'S 146°33'E; grid ref. DU 532427).

SITE D: wet sclerophyll forest (TOF) and closed forest (CF) (Bluewater State Forest). This transitional habitat is very narrow and patchy and not readily distinguished in air photos. Dominant tree species are *Syncarpia glomulifera*, *Allocasuarina* sp. and *E. grandis* and there are also several other eucalypts and a variety of rainforest species. The rainforest species often form a shrub layer under the emergent sclerophyll species. This habitat represents an ecotonal area between rainforest and the open eucalypt forest to the west. Three sub-sites were selected on the basis of differing vegetation structure: D1 - closed *Allocasuarina*/*Syncarpia* forest with dense shrub layer and very little ground cover (19°14'S 146°24'E; grid ref. DU371734); D2 - *Allocasuarina*/*Syncarpia*/*Eucalyptus* forest with some shrubs (predominantly rainforest species) and short, dense grass (19°14'S 146°23'E; grid ref. DU 365731); D3 - *Syncarpia*/*E. grandis*/*Allocasuarina* forest with dense ground cover of blady grass and sedges and also some patches of dense shrubs (19°14'S 146°23'E; grid ref. DU 359725). D4 - *Allocasuarina*/*Eucalyptus* open forest with dense ground cover of *Xanthorrhoea*, *Imperata* and areas of shrubs. *Pandanus* sp. occur in low lying wetter areas. A rainforest sub-site was not sampled due to previous survey work on Mount Halifax which is less than 1 km outside the study area (Williams et al., 1993).

SITE E: open Forest (OF) (19°17'S 146°22'E) on the western side of the Bluewater range. This site is a transitional zone between the dense, wet sclerophyll forest of site D and the eucalypt woodland of site B. The vegetation grades from Tall Open forest with *Eucalyptus grandis*, *Syncarpia glomulifera* and *Allocasuarina torulosa* dominants, through a mixed eucalypt open forest (*E. citriodora*, *E. peltata*, *E. shirleyi* and others) to Ironbark woodland near West Keelbottom creek. Riparian vegetation along the creek consists of patches of closed *Tristaniaopsis exiliflora* gallery forest and more open *Callistemon* spp./*Melaleuca* spp. forest. Further upstream there are several vine thickets, which were investigated. The various areas sampled at this site have been combined because of their close proximity and because the site was only sampled once.

Major terrestrial habitat types and associated samples were therefore as follows:

Open woodland: A2, A3, B1, B3

Open forest: B4, C1, C4, D4, E

Tall open forest/closed forest: D1, D2, D3

Riparian: A1, B2, C2, E

TABLE 1. Fish sampling sites and their major physical characteristics. Ref, grid reference, 1:100000 series; Hbt, habitat (P = pool, R = riffle); Temp, temperature (C); D.O., dissolved oxygen (mg/L); Cond, conductivity ($\mu\text{S}/\text{cm}$); Dpth, maximum depth (cm); Wdth, maximum width (m); Subst, major substratum (B = bedrock, RR = large rocks, R = small rocks, G = gravel, S = sand, L = leaf litter; % indicates proportion of substrate damaged by hoofed animals); Curr, current velocity (cm/s); Vegetation: Mel = riparian *Melaleuca* overhanging, W = ironbark woodland, Cal = riparian *Callistemon*, OF = open *Eucalyptus* forest. CF = closed forest.

Site	Ref	Hbt	Temp	D.O.	Cond	pH	Dpth	Wdth	Subst	Curr	Vegetation
1 Star	DU126841	P	22.3	6.7	108	6.9	40	12	RR,R,G,S	3	Mel, wdInd
		R	22.2	7.1	101	7.0	18	9	R,S	6	Mel, wdInd
2 Little Star	DU151635	P	19.5	7.0	221	7.4	200	15	R,S		Mel, wdInd
		R	19.8	7.0	213	7.1	18	3	R,G,S	15	Mel, wdInd
3 Star	DU084681	P	-	-	-	-	-	200	75	S,L	0
				23.6	8.3	-	-	-			
				21.6	11.8	58	8.3 0.3				%
4 Little Star	DU120617	P	20.2	8.8	176	7.6	50	5	R,S,L	0	MelwdInd
		R	20.5	8.9	163	7.5	15	5	R,S		-
5 Keelbottom	DU247293	P	22.6	-	420	7.9	30	5		R,S,L	0
		R	22.0	8.4	437	7.9	25	4	RR,R,G,S,L	10	
6 Keelbottom	DU301448	P	20.7	7.3	465	7.6	40	3	R,S	0	Mel, OF
		R	21.0	7.9	393	7.7	35	6	R,G,S	30	
7 Reid	DU598275	P	28.1	5.1	671	8.6	400	15	B	0	Mel,Cal,OF
		R	26.0	6.8	-	8.1	6	1			R
			23.6	8.3	411	7.7 150		<10%			
8 Fanning	DU421346	P	22.9	7.3	957	8.4	60	10	R,S,L	2	Mel,OF
		R	24.5	7.3	1240	8.8	20	3	R	50	Mel,OF
9 Stake	DU480481	P	22.5	8.1	164	8.4	35	12	R,G,S,L	0	Mel,Cal,OF
10 Little Star	DU334808	P	14.0	11.1	42	-	35	6	R,S,L	0	CF
		R	13.0	10.4	48	7.2	15	5	RR,R,S	20	
11 Keelbottom	DU341786	P	15.5	8.3	42	5.7	25	4	RR,R,S,L	0	CF
		R	14.8	8.0	44	5.4	25	4	R,S	30	CF
			20.0	6.4	37	6.5 180		<10%			
12 Dtswd wetInd	DU248290		-	-	-	-	-		10-30%		
13 Dtswd dam	DU272272		27.2	9.7	102	8.8	40		30-70%		
14 Dtswd dam	DU275256		24.7	9.2	94	8.5	220		<10%		
15 L.Star Ponto DU244700		21.9	10.7	118	8.2	30				%	
16 Star Stn.dam	DU134605		23.3	8.2	187	8.3 180				%	
17 Star	DU272865		20.0	6.4	37	6.5 180					

Rocky outcrops: C3

Observations were not restricted to these sites, however, and our records are supplemented by information from extensive observations across the study area. For example, while there was only

one rocky outcrop sampling site, general observations were made wherever rocky outcrops were encountered, and are incorporated in our composite species lists.

The extent of some habitat types did not warrant

the status of major sites, and were therefore only sampled opportunistically. For example, grassland had mostly been previously cleared land and was not extensive.

STREAMS

Because of the highly seasonal climate, the streams are seasonal, and surface flow ceases in most of them in the dry season. However, most of the streams have permanent pools. The streams range from upland, rocky, high gradient channels under complete canopy cover to the low gradient, open sandy channels on the south western plain.

Seventeen major sites were selected (Fig. 2) to represent stream and other wetland types across the study area. The grid references and major physical features of the sites are listed in Table 1. In April the streams were running well. In the second survey (September 1991) most streams had ceased to flow and remained only as pools.

The major stream sites were located, from north west to south east, on the Star River (sites 1 and 3), the Little Star River (sites 2, 4 and 10), Keelbottom Creek (sites 5, 6 and 11), Fanning River/Stake Creek (sites 8 and 9) and Reid River (site 7).

The data in Table 1 broadly illustrate the range of sites sampled, from the low pH, low conductivity, cool rainforest streams in the north (sites 10 and 11) to the warmer, high pH, high conductivity woodland streams in the south east (sites 7, 8 and 9). Differences between the sites reflect several variables, including climate and vegetation, and geology. For example, the streams in the south east included deposits of calcium carbonate in their catchments, which leads to the alkaline water with high conductivity, while those in the rainforest were based on granitic bedrock and soils and had low levels of dissolved substances in them.

SAMPLING METHODOLOGY

TERRESTRIAL FAUNA

The sampling strategy was designed to capture or observe the highest diversity of vertebrates possible. Given the time constraints, assessments of absolute densities were given lower priority. A variety of techniques were employed, all of which proved to be useful. Sampling effort was standardised in order to render intersite data as comparable as possible. However, differences in weather, terrain and vegetation all affect the efficiency of sampling. These effects include greater difficulty of observation within dense forest, re-

duced visibility and/or animal activity during periods of rain or heavy mist, reduction of frog and reptile activity as the weather became cooler and drier, and inability to sample intensively in areas where vehicular access was not possible.

Two surveys were conducted: 8 April-3 May 1991 (sites A-D); and 7 August-25 October 1991 (sites A-E). A total of 63 days were spent in the field (approximately 146 person days).

Literature consulted to aid identification were Strahan (1983), Cogger (1986), Hall and Richards (1979), Kitchener and Caputi (1985), Simpson and Day (1984), and Pizzey (1980).

TRAPPING

Three trapping techniques were utilised:

Elliot traps - 100 Elliot traps (type A), divided equally between the sub-sites, were set over three or four nights at each site. Traps were set 10m apart and alternatively baited with oats and vanilla essence, or oats and peanut butter or oats/peanut butter/sardines. These traps are designed for capturing mammals up to the size of rats. Twenty 20 cage traps (bandicoot size) were set with the Elliot traps, equally divided among sub-sites and equally spaced along the trapping lines. These traps were baited with sardines, rolled oats and vanilla essence and were designed to capture medium-sized mammals, e.g. *Isodon macrourus*. Additionally, 20 large cage traps (cat size) were used at site D in the rainforest. These traps were baited with meat, in an attempt to capture large predators, specifically quolls (*Dasyurus maculatus*), which were known from anecdotal evidence to have occurred at Paluma at least until the 1950's.

Pit traps are suitable for capturing a variety of small mammals, reptiles and amphibians and 30 (20 litre drums) were installed at sites A and B. Five drift fences 10m long and each with two pits were set up at each sub-site (i.e. 10 pits per sub-site \times 3 sub-sites = 30 pits and 150m of drift fence per site) at sites A and B. Pit trapping had also been conducted previously in rainforest on Mt Halifax, just outside the study area (Williams et al., 1993). Pit traps were not used on the other sites because it was found during the first survey of sites A and B that the results were not sufficient to justify the time spent installing them.

SPOTLIGHTING

Spotlighting was conducted every night in the field and totalled eight nights per site. Each sub-site was spotlighted at least one night per trip for approximately 1.5hr. Additionally general sur-

TABLE 2. The diversity of vertebrate fauna within the study area. Species previously recorded in the region and which possibly occur within the study area are included (sources of previous records include Lavery & Johnson 1968, 1969, Blakers *et al.* 1984, Winter 1984, Queensland Museum records, QNPWS Mt Spec species list, Garnett (pers. comm.). Sources of possible records are Strahan, 1983; Cogger, 1986; Readers Digest, 1976; Simpson and Day, 1984. Species listed as previously recorded have not necessarily been recorded within the study area, but have been recorded in the near vicinity. Only records of species which are likely to be present (on the basis of available habitat types) have been included.

TAXONOMIC GROUP	OBSERVED	PREVIOUSLY RECORDED/POSSIBLE
MAMMALS		
# Families	18	21
# Species	57	63/76
BIRDS		
# Families	52	65
# Species	100	152/152
REPTILES		
# Families	3	6
# Species	5	64/111
AMPHIBIANS		
# Families	1	1
# Species	1	1/2
FISH		
# Families		
# Species		

veys were conducted at each site. Most of the spotlighting was conducted along tracks using a 150w handheld spotlight from a vehicle, this being the best method for arboreal mammals in the open woodland. Walking transects, using two 30w handheld spotlights and low power torches were conducted in areas inaccessible by vehicle (e.g. along the creeks) and in areas of denser vegetation.

MIST-NETTING

Mist netting was undertaken every night in the field to capture bats, but was limited by time and the availability of suitable sites, namely potential flight corridors and water bodies. Netting was conducted for about 2hr commencing at dusk. The nets were usually set above a suitable creek or dam, or across a road (in rainforest at Bluewater). Sites netted were: Keelbottom creek (site A, 19°37'S, 146°17'E; grid ref. DU 247293); Cockatoo dam (site A, 19°34'S, 146°15'E; grid ref. DU 206359); Sandy creek (site A, 19°30'S, 146°15'E; grid ref. DU 215339); Little Star river (site B, 19°18'S, 146°12'E; grid ref. DU 151635); Dinner

Creek (site B, 19°23'S, 146°11'E; grid ref. DU 154566); Star River (site B, 19°17'S, 146°07'E; grid ref. DU 081670); Stake Creek (site C, 19°27'S, 146°30'E; grid ref. DU 479481); Dip Creek (site C, 19°26'S, 146°32'E; grid ref. DU 509511); Keelbottom creek - Bluewater (site D, 19°14'S, 146°23'E; grid ref. DU 365731); Bluewater forestry road (site D, 19°14'S, 146°24'E; grid ref. DU 375732); unnamed creek (Star 8159-3, 19°30'S, 146°15'E; grid ref. DU 206443).

BIRDS

Bird species were recorded on a daily basis using several methods. Early morning (dawn) observations were made at each site using both calls and direct observation. Observations were also made while clearing the trapping lines each morning. Each sub-site was also sampled by at least one complete afternoon of bird censusing. Nocturnal birds were recorded using calls and during spotlighting transects. All incidental bird observations were also recorded. Any accessible dams or swamps were visited to record water birds.

ACTIVE SEARCHING

Active searching is simply a collective term for a number of activities aimed at finding and capturing cryptic fauna. This includes miscellaneous observations from vehicles or on foot, as well as rolling logs and rocks, searching under bark and inside hollow limbs of dead trees, capturing by hand any lizards or snakes seen, searching hollow trees and under bridges for bats, and searching any piles of tin or timber. These activities are difficult to standardise, but nevertheless are very useful in supplementing species records (especially reptiles).

While every effort was made to standardise sampling within and between sites, it should be noted that spatial and temporal variation in climate, geography and vegetation affected the visibility and/or catchability of different species as well as imposing differing logistic constraints on our sampling routine. For example, at site E, vehicle access was extremely limited and so sub-sites were much closer together than at other sites.

Fish sampling was done at 11 stream sites and during both surveys, in April and September. Four sampling methods were used:

Seine netting: pools were swept 2-5 times using an 8.0m seine of 10mm mesh. The success of the seine netting was variable, depending on the physical characteristics of the individual pools.

TABLE 3. Number of species of terrestrial vertebrates (excluding feral species) observed during field surveys of the study area by site (habitat).

	SITE A	SITE B	SITE C	SITE D	SITE E
	Ironbark Woodland	Mixed Eucalypt Forest	Wet Sclerophyll Forest	Mixed OF/W	
MAMMALS	27	15	22	16	10
Ex bats	14	11	15	10	8
BIRDS	79	84	82	92	52
Ex open water	79	64	70	90	49
REPTILES	13	8	13	15	8
AMPHIBIANS	9	8	8	4	5
TOTAL	128	115	125	127	75

However, most of the small active fish were recorded using the seine nets.

Fixed net: a 50m fixed net (50mm mesh) was employed at any site which had a large enough pool. The fixed net was useful in catching some of the larger fish and turtles.

Baited lines: baited lines were used in larger pools and were also useful in catching some of the larger species of fish, turtles and eels.

Dip net: weed beds and snags were swept with a hand held dip net to catch small fish such as gudgeons, ambassids, hardyheads and catfish.

Following identification, fish were returned to the water.

In general no voucher specimens were taken. However, specimens of difficult to identify species were taken and checked by dissection (small mammals and fish). The small mammals (*Rattus fuscipes*, *Melomys cervinipes*, and *M. burtoni*) were sent to the Queensland Museum.

RESULTS AND DISCUSSION

A total of 297 species of vertebrates from 91 families were recorded during the fauna surveys. This diversity is not surprising considering the large area and the diversity of habitats included in the area. High diversities of mammals (50 species) and birds (180 species) were recorded, but the diversities of reptiles and amphibians were certainly underestimated because the surveys were conducted outside the wet season. Table 2 summarises the diversity of vertebrate fauna by major taxonomic groups including those species previously recorded in the region and which are likely to occur within the study area.

Table 3 summarises the diversity of terrestrial vertebrates observed by site. In effect, this partly summarises diversity by habitat type, as sites A and B represent Ironbark woodland, site C represents the mixed eucalypt open forest, and sites D and E are a mixture of closed forest and tall open

forest (i.e. the transitional zone between rainforest and open forest).

Total numbers of terrestrial vertebrates was surprisingly similar for sites A, B, C and D. The diversity was lowest at site E, but this was primarily due to a lower sampling intensity.

MAMMALS

The 50 species recorded during the surveys (Appendix 1), plus the 11 extra species from other records represent a large proportion (80%) of approximately 76 species that might possibly occur in the area. Mammal diversity was highest in the more open woodland and eucalypt forests of sites A, B and C. This was due to higher observed diversities of bats, arboreal marsupials and macropods in the open forest/woodland sites.

BIRDS

Bird diversity was highest in the wet sclerophyll forest of site D. The higher bird diversity of this forest is especially noticeable if waterbirds are removed from consideration. The number of species recorded during this study (180) (Appendix 1) represents 64% of the 282 species known from all sources to occur in, or in similar habitats close to, the study area. Given (i) the extent and duration of the survey, (ii) the high mobility of birds (which usually leads to a large number of vagrants being recorded in geographical species lists) and (iii) the absence of a number of summer species during the period of field work, this species count is high.

A sighting of a Grey Falcon in open forest at site E was the only observation of a bird listed as rare. Two other rare species previously recorded in the vicinity are the Red Goshawk and Square-tailed Kite. Southern Cassowaries are presently listed as vulnerable.

There are 13 species of bird which are endemic to the north Queensland tropical rainforest (Crome & Nix 1991), and 11 of these were observed during the survey: Mountain Thornbill,

Bridled Honeyeater, Macleay's Honeyeater, Pied Monarch, Bowers Shrike-thrush, Grey-headed Robin, Northern Logrunner, Victoria's Riflebird, Fernwren, Tooth-billed Bowerbird and the Lesser Sooty Owl. An additional species, the Golden Bowerbird, has been previously recorded in the vicinity. Of the 13 species of rainforest endemics, only the Atherton Scrubwren is not likely to be present.

Of ten subspecies endemic to north Queensland (Crome & Nix, 1991) nine were observed within the study area during this study. These were the northern subspecies of King parrot, Pale-yellow Robin, Yellow-breasted Boatbill, Grey Fantail, Eastern Whipbird, Brown Warbler, Northern Catbird, Satin Bowerbird and Boobook Owl (Crome & Nix, 1991).

REPTILES

Reptiles recorded during the study area surveys are listed in Appendix 1. The 38 species observed represent 59% of the 64 species recorded from the study area and its immediate environs. It is likely that a large number of reptile species present in the study area were not recorded because of their cryptic behaviour and lower activity levels in the dry season. Nevertheless, the species list in Tables 6 represent a substantial diversity of reptiles, distributed fairly evenly among wooded habitats.

AMPHIBIANS

Amphibian diversity appears to be highest in the open forest/woodland sites, primarily the riparian sub-sites, but this result could change considerably if a wet season amphibian survey was undertaken. Despite the rather poor conditions for observing amphibians, 16 species were recorded for the study area (Appendix 1) with Queensland Museum records increasing the total to 22 species. Most species were recorded in the riparian zones and at dams. However, it is likely that in the early wet season greater numbers of frogs would be observed in the areas away from permanent creeks.

No rare or uncommon species of amphibians were recorded. However, two species of rainforest endemic frogs were recorded (*Cophixalus ornatus* and *Sphenophryne robusta*), and two other species have been recorded previously and are likely to be present (*Nyctimistes dayi* and *Mixophyes schevilli*).

FISH

Fish species recorded in the two surveys are shown in Appendix 1. All, apart from the Eel, are

regarded as principal freshwater species, meaning that they undergo their whole life cycle in fresh water. The eel is diadromous, i.e. it has to migrate to the sea to breed.

Diversity at each site varied according to the size of the stream. In the small rainforest streams either no fish were found (site 11) or only the Purple-spotted Gudgeon occurred (site 10). This is similar to the pattern in other rainforest streams: for example, other than the eel, there are no fish in Birthday Creek (R.G. Pearson, unpubl. data) and only the gudgeon in Yuccabine Creek (Pearson et. al., 1986). Further downstream, the sites had a larger complement of fish species with the addition rather than replacement of species - as is the case elsewhere, eg. the Annan River, near Cooktown (Hortle & Pearson, 1990).

It is of interest to compare the diversity of fishes between systems. This is best done using principal freshwater species, and by referencing the sizes of catchment areas, because larger catchments tend to accommodate more species (Welcomme, 1979). The area of the Star catchment sampled was about 1100km², that of Keelbottom Creek also about 1100km², and that of the upper Fanning River about 200km² (Qld Water Res. Comm. data). The fish survey recorded, respectively, 10, 8 and 8 principal freshwater species from these systems, and a total of 11 species. This compares with 12 species in the Black and Alice Rivers (about 300km²) near Townsville (Beumer, 1980) and 15 species in the Annan River (about 1000km²) (Hortle & Pearson, 1990). These figures are based on two years' monthly sampling of five sites in the Black/Alice and two sets of samples from 17 sites in the Annan. Comparison with middle Burdekin River samples (Pearson, 1991a) shows that there are only a few extra species recorded or missing from the river.

Given the different sampling intensities and catchment areas of the different systems, it appears that diversity of the fish fauna in the study area compares favourably with other stream systems in northern Queensland. Most of the species recorded have a broad distribution in eastern or northern Australia. Allen (1989) lists species within different status categories (endangered, vulnerable, potentially threatened, indeterminate, restricted and uncertain). The only species to appear on any of these lists and in the records from the study area streams is the Small-headed Grunter, which is listed as restricted. This species is only known from the Burdekin River system. It was not collected during the present survey, but Pusey (pers. comm.) has collected it from Run-

ning River, near the study area, and Pearson (1991b) recorded it from the middle Burdekin River. Otherwise there is no indication of any species of threatened status in the study area. However, samples of gudgeons, provisionally ascribed to *Hypseleotris compressa*, are currently under review.

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Part 1. Mammal species of the study area. The table lists numbers observed during the April/May field trips (nos. before the “/”) and the August/September field trips (nos. after the “/”). A - Open woodland (Ironbark) in the southern study area, B - Open woodland (Ironbark) northern study area, C - Open Eucalypt forest (High Range training area), D - Wet sclerophyll/mixed open forest at the R.A.A.F. training area at Bluewater State forest, E - Transitional area between the Wet sclerophyll forest of site D and the open woodland of site B. Observational techniques include E - Elliot traps, C - Cage traps, P - Pits traps, H - by hand, S - spotlighting/miscellaneous observation, F - faecal pellets, M - mist netting, * - presence recorded, but not counted. Species names follow Ingram & Raven (1991).

SPECIES	COMMON NAME		A	B	C	D	E
Tachyglossidae							
<i>Tachyglossus aculeatus</i>	Short beaked Echidna	S	-/1	/	-/	-/	-
Dasyuridae							
<i>Antechinus flavipes</i>	Yellow-footed Antechinus	EPHS	-/	-/	-/	2/1	1
Peramelidae							
<i>Isodon macrourus</i>	Northern Brown Bandicoot	CES	/	2/2	1/5	-/3	
<i>Perameles nasuta</i>	Long-nosed Bandicoot	CS	/	-/	-/	3/2	2
Phascolarctidae							
<i>Phascolarctus cinereus</i>	Koala	S	-/	3/	/	/	
Petauridae							
<i>Petaurus breviceps</i>	Sugar Glider	S	1/2	/1	1/1	-/1	1
<i>Petaurus norfolcensis</i>	Squirrel Glider	S	-/	-/	7/2	/	-
Pseudocheiridae							
<i>Petauroides volans</i>	Greater Glider	S	3/4	5/10	15/12	/	5
<i>Pseudocheirus peregrinus</i>	Common Ringtail Possum	S	-/	-/	19/15	-/	1
Phalangeridae							
<i>Trichosurus vulpecula</i>	Common Brushtail Possum	SC	1/1	1/	19/17	/	3
Potoroidae							
<i>Aepyprymnus rufescens</i>	Rufous Bettong	CS	1/6	3/7	/	-/	1
Macropodidae							
<i>Macropus agilis</i>	Agile Wallaby	S	5/1	/	-/	-/	
<i>Macropus giganteus</i>	Eastern Grey Kangaroo	S	6/5	-/20	2/*	/	-
<i>Macropus parryi</i>	Whiptail Wallaby	S	/2	-/3	-/	/	
<i>Macropus robustus</i>	Wallaroo	S	-/2	1/	2/*	-/	
<i>Petrogale assimilis</i>	Allied Rock Wallaby	CSF	/3	-/	1/5	/	
<i>Wallabia bicolor</i>	Swamp Wallaby	S	-/1	-/	-/	/	
Pteropidae							

SPECIES	COMMON NAME		A	B	C	D	E
<i>Nyctimene robinsoni</i>	Queensland Tube-nosed Bat	M	1/-	-/-	-/-	/	-
<i>Pteropus alecto</i>	Black Flying-fox	S	1/-	-/*	-/-	/	-
<i>Pteropus scapulatus</i>	Little Red Flying-fox	S	/1	-/*	-/6	-/3	-
<i>Syconycteris australis</i>	Queensland Blossom-bat	M	-/-	-/-	-/-	-/1	
Molossididae							
<i>Mormopterus loriae</i>	Little Northern Mastiff-bat	M	3/-	-/-	-/-	/-	
Rhinolophidae							
<i>Rhinolophus megaphyllus</i>	Eastern Horseshoe-bat	H	-/-	-/-	-/1	-/-	-
<i>Rhinolophus philipinensis</i>	Large-eared Horseshoe-bat	M	-/-	/	/1	-/-	-
Vespertilionidae							
<i>Chalinobius gouldii</i>	Gould's Wattled Bat	M	4/4	-/-	-/3	/	-
<i>Chalinobius morio</i>	Chocolate Wattled Bat	M	-/1	-/-	-/-	-/-	-
<i>Chalinobius nigrogriseus</i>	Hoary Bat	M	3/2	/	-/-	-/-	-
<i>Miniopterus australis</i>	Little Bent-wing Bat	M	-/-	-/-	-/1	1/1	-
<i>Miniopterus schreibersii</i>	Common Bent-wing Bat	HM	1/1	-/-	/2	-/3	
<i>Myotis adersius</i>	Pond Bat	M	6/-	-/-	-/-	-/2	2
<i>Nyctophilus bifax</i>	North-Queensland Long-eared Bat	M	1/	-/-	-/1	-/1	2
<i>Nyctophilus geoffroyi</i>	Lesser Long-eared Bat	M	-/-	-/3	-/-	/-	
<i>Scoteanax rueppellii</i>	Greater Broad-nosed bat	M	8/-	/	-/-	-/-	
<i>Scotorepens balstoni</i>	Western Broad-nosed bat	M	-/1	/1	/-	-/-	
<i>Scotorepens sanborni</i>	Little Northern Broad-nosed bat	M	-/1	/1	/	-/-	-
Leporidae							
<i>Oryctolagus cuniculus</i>	Rabbit	S	5/2	- /2+	1+/*	/	-
Muridae							
<i>Hydromys chrysogaster</i>	Water Rat	CS	3/*	4+/*	2/2	-/1	
<i>Melomys burtoni</i>	Grassland Melomys	E	-/-	-/-	4/2	3/2	-
<i>Melomys cervinipes</i>	Fawn-footed Melomys	CE	-/-	/	9/6	16/12	
<i>Pseudomys gracilicaudatus</i>	Eastern Chestnut Mouse	E	2/2	1/1	3/2	-/-	/3
<i>Rattus fuscipes</i>	Bush Rat	EC	-/-	/	-/-	28/9	
<i>Rattus lutreolus</i>	Swamp Rat	E	-/-	-/-	/	3/2	-
<i>Rattus rattus</i>	Black Rat	EC'S	4/-	-/-	1/1	/-	-
<i>Uromys caudimaculatus</i>	White-tailed Rat	CSE	-/-	/	-/-	5+/-	-
<i>Zyzomys argurus</i>	Common Rock-rat	E	-/-	/	4/5	-/-	-
Canidae							
<i>Canis familiaris dingo</i>	Dingo	S	*/*	1/*	1/-	-/-	
Felidae							

APPENDIX 1 cont.

SPECIES	COMMON NAME		A	B	C	D	E
<i>Felis catus</i>	Feral Cat	S	-/1	-/2	-	-	-
Equidae							
<i>Equus caballus</i>	Feral Horse	S	-	-	-/2	-	-
Suidae							
<i>Sus scrofa</i>	Feral Pig	SE	-/2	-/2	-/2	-/2	-

Part 2. Bird species of the study area. The index of abundance is based on the following criteria: (-) not observed at this site; 1 - observed on one occasion during the field trip; 2 - observed several times; 3 - common, observed most days; 4 - abundant, observed a number of times every day, usually at several different places. Names follow Ingram & Raven (1991). For further explanation see Part 1.

SPECIES	COMMON NAME		A	B	C	D
Ciconiidae						
<i>Casuarus casuarinus</i>	Southern Cassowary		-/1	-/1	-	-/1
<i>Dromaius novaehollandiae</i>	Emu		-/2	1/2	-/1	-/1
Podicipedidae						
<i>Podiceps cristatus</i>	Crested Grebe					
<i>Polycephalus polycephalus</i>	Hoary-headed Grebe		1/1	1/1	-/1	-/1
<i>Tochybaptus novaehollandiae</i>	Australasian Grebe		2/1	1/1	-/1	-/1
Phalacrocoracidae						
<i>Phalacrocorax carbo</i>	Great Cormorant					
<i>Microcarbo melanoleucos</i>	Little Pied Cormorant		-/1	3/1	-/2	-/1
<i>Hypoleucos sulcirostris</i>	Little Black Cormorant		-/1	1/1	-/1	-/1
Anhinga						
<i>Anhinga novaehollandiae</i>	Australian Darter		-/1	1/1	-/2	-/1
Ardeidae						
<i>Casmerodius alba</i>	White Egret		1/1	1/1	-/1	-/1
<i>Egretta intermedia</i>	Plumed Egret		3/1	2/1	-/1	-/1
<i>Ardea novae-hollandiae</i>	White-faced Heron		-/1	-	-/3	-/1
<i>Ardea pacifica</i>	White-necked Heron		1/1	1/1	1/1	-/1
<i>Butor flavicollis</i>	Black Butor		1/1	-/1	-/1	-/1
<i>Nycticorax nycticorax</i>	Nankeen Night Heron		-/1	-/1	-/1	-/2
Threskiornithidae						
<i>Platalea flavipes</i>	Yellow-billed Spoonbill		1/1	-/1	-/1	-/1
<i>Platalea regia</i>	Royal Spoonbill		-/1	-/1	-/1	-/1
<i>Threskiornis spinicollis</i>	Straw-necked Ibis		-/1	2/3	-/1	-/1
Anatidae						
<i>Anas gracilis</i>	Grey Teal		1/1	1/1	-/1	-/1
<i>Anas superciliosa</i>	Black Duck		1/1	3/1	2/2	-
<i>Aythya australis</i>	White-eyed Duck		-/1	-/1	-/1	-
<i>Chenonetta jubata</i>	Wood Duck		2/1	1/1	1/1	-
<i>Dendrocygna arcuata</i>	Wandering Whistling-Duck		2/1	2/1	2/1	-

SPECIES	COMMON NAME		A	B	C	D
<i>Nelephus coromandelianus</i>	White Pygmy-Goose		1/1	-/1		-
Accipitridae						
<i>Accipiter cirrocephalus</i>	Collared Sparrowhawk		-	-	-	1
<i>Accipiter fuscatus</i>	Brown Goshawk		-		1/1	1/1
<i>Accipiter novaehollandiae</i>	Grey Goshawk		-	-	-	1/1
<i>Aquila audax</i>	Wedge-tailed Eagle		2/2	-	2/2	-
<i>Aviceda subterminalis</i>	Crested Hawk		1/1	3/1	-	1/1
<i>Circus assimilis</i>	Spotted Harrier					
<i>Elanus noatus</i>	Black-shouldered Kite		-/1	-/1	1/1	-/1
<i>Haliaeetus leucogaster</i>	White-bellied Sea-Eagle		-/1	1/1	-/1	-/1
<i>Hieraaetus morphnoides</i>	Little Eagle		-/1	-/1	1/1	-/1
<i>Milvus migrans</i>	Fork-tailed Kite		-/1	-/1	1/1	-/1
<i>Haliaeetus leucogaster</i>	Whistling Kite		1/2	3/3	1/1	-/1
Falconidae						
<i>Falco berigota</i>	Brown Falcon		1/1	1/1	1/1	-/1
<i>Falco cenchroides</i>	Nankeen Kestrel		1/1	1/2	1/2	-/1
<i>Falco hypoleucos</i>	Grey Falcon		-	-	-	-
<i>Falco longipennis</i>	Little Falcon		-	1/1	-	-
Meleptidae						
<i>Meleptus lathamii</i>	Brush Turkey		-		1/1	2/1
Phasianidae						
<i>Synotis australis</i>	Brown Quail		-/1	1/2	1/1	-/1
Gruidae						
<i>Grus rubicundus</i>	Brolga		-	1/1	-	-
Rallidae						
<i>Fulica atra</i>	Eurasian Coot		1/1	1/1	-	-
<i>Gallinula tenebrosa</i>	Dusky Moorhen		1/1	1/1	-/1	-/1
<i>Rallina tricolor</i>	Red-necked Crake		-/1	-/1	-/1	-/1
Otididae						
<i>Ardeotis australis</i>	Australian Bustard				1/1	
Iacidae						
<i>Irediparra galinae</i>	Comb-crested Jacana		1	1/1	-	-
Burhinidae						
<i>Burhinus grallarius</i>	Bush Thick-knee		2/1	-/1	1/2	2
Charadriidae						
<i>Elseornis melanope</i>	Black-fronted Plover		1		-	-
<i>Vanellus miles</i>	Masked Lapwing (Plover)		1/1	-/3	1/1	-/1
Columbidae						
<i>Chalcophaps indica</i>	Green-winged Pigeon		-/1	-/1	-/1	2
<i>Columba leucocoma</i>	White-headed Pigeon		-	-	-	1/1
<i>Geopelia pluvialis</i>	Peaceful Dove		-	2/3	3/3	-
<i>Oxyphaps lophotes</i>	Crested Pigeon		4/1	4/4	1/1	-
<i>Petrophassa carpalis</i>	Squatter Pigeon		-	2/3	1/1	-

APPENDIX 1 cont.

SPECIES	COMMON NAME		A	B	C	D
<i>Todirhamphus macleayi</i>	Forest Kingfisher		-/-	-/-	2/2	-/2
<i>Todirhamphus pyrrhopygius</i>	Red-backed Kingfisher		-/-	1/-	-/-	-/-
<i>Todirhamphus sanctus</i>	Sacred Kingfisher		1/-	1/-	-/1	-/-
Meropidae						
<i>Merops ornatus</i>	Rainbow Bee-eater		2/-	-/-	3/-	1/3
Pittidae						
<i>Pitta versicolor</i>	Noisy Pitta		-/-	-/-	-/-	1/2
Campephagidae						
<i>Coracina novaehollandiae</i>	Black-faced Cuckoo-Shrike		2/2	3/1	3/2	-/1
<i>Coracina papuensis</i>	Little Cuckoo-Shrike		2/3	1/-	-/1	1/2
<i>Lalage leucomela</i>	Varied Triller		-/-	-/-	-/-	1/1
Orthonychiidae						
<i>Orthonyx spaldingii</i>	Northern Logrunner		-/-	-/-	-/-	3/2
<i>Psophodes olivaceus</i>	Eastern Whipbird		-/-	-/-	-/-	4/2
Pomatostomidae						
<i>Pomatostomus temporalis</i>	Grey-crowned Babbler		1/3	1/2	-/-	-/-
Sylviidae						
<i>Cinchorhamphus mathewsi</i>	Rufous Songlark		2/1	1/-	-/-	-/-
<i>Megalurus timoriensis</i>	Tawny Grassbird		-/-	-/-	-/-	-/-
Maluridae						
<i>Malurus melanocephalus</i>	Red-backed Wren		1/-	-/-	3/3	-/2
Acanthizidae						
<i>Acanthiza katherina</i>	Mountain Thornbill		-/-	-/-	-/-	1/-
<i>Acanthiza nana</i>	Little Thornbill		1/3	1/2	-/-	-/-
<i>Oreoscopus gutturalis</i>	Fernwren		-/-	-/-	-/1	-/-
<i>Gerygone fusca</i>	Western Warbler		1/-	-/-	-/-	-/-
<i>Gerygone mouki</i>	Brown Warbler		-/-	-/-	-/-	3/-
<i>Gerygone olivacea</i>	White-throated Warbler		-/-	-/1	-/1	-/-
<i>Gerygone palpebrosa</i>	Fairy Warbler		-/-	-/-	-/1	1/1
<i>Sericornis citreogularis</i>	Yellow-throated Scrubwren		-/-	-/-	-/-	-/1
<i>Sericornis frontalis</i>	White-browed Scrubwren		-/-	-/-	-/-	1/1
<i>Sericornis magnirostris</i>	Large-billed Scrubwren		-/-	-/-	-/-	1/1
Monarchidae						
<i>Arses kaupi</i>	Pied Monarch		-/-	-/-	-/-	4/1
<i>Machaerirhynchus flaviventer</i>	Yellow-breasted Boatbill		-/-	-/-	-/-	1/1
<i>Monarcha trivirgatus</i>	Spectacled Monarch		-/-	-/-	-/1	4/3
<i>Myiagra cyanoleuca</i>	Satin Flycatcher		-/-	-/-	1/1	1/-
<i>Myiagra rubecula</i>	Leadend Flycatcher		-/-	1/-	1/4	-/2
<i>Rhipidura fuliginosa</i>	Grey Fantail		4/4	4/3	4/4	4/2
<i>Rhipidura leucophrys</i>	Willie Wagtail		3/3	4/3	2/-	-/-

SPECIES	COMMON NAME		A	B	C	D
<i>Macropygia phasianella</i>	Brown Pigeon		-/-	-/-	-/-	1/-
<i>Phaps chaloptera</i>	Common Bronzewing		/2	1/-	/	/
<i>Ptilinopus magnificus</i>	Wompoo Pigeon		-/-	/	/	/2
<i>Ptilinopus superbus</i>	Purple-crowned Pigeon		-/-	-/-	-/-	-/2
Loriidae						
<i>Trichoglossus chlorolepidotus</i>	Scaly-breasted Lorikeet		-/-	-/-	1/2	-/2
<i>Trichoglossus haematodus</i>	Rainbow Lorikeet		3/4	1/3	3/3	1/3
Cacatuidae						
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo		3/3	4/3	-/1	1/3
<i>Calyptrorhynchus magnificus</i>	Red-tailed Black Cockatoo		1/1	-/-	1/-	2/1
Psittacidae						
<i>Alisteria scapularis</i>	King Parrot		-/-	-/-	-/-	-/1
<i>Aprosmictus erythropterus</i>	Red-winged Parrot		1/2	1/1	-/1	-/-
<i>Platycercus adscitus</i>	Pale-headed Rosella		3/2	4/3	3/2	-/-
<i>Platycercus elegans</i>	Crimson Rosella		-/-	-/-	-/-	1/-
Cuculidae						
<i>Centropus phasianinus</i>	Pheasant Coucal		2/1	3/3	2/1	-/1
<i>Chrysococcyx basalis</i>	Horsfield's Bronze-Cuckoo		-/-	-/-	/1	1/-
<i>Chrysococcyx russatus</i>	Rufous-breasted Bronze-Cuckoo		/	/	-/-	1/
<i>Chrysococcyx lucidus</i>	Shining Bronze-Cuckoo		/	/	/	1/
<i>Cacomantis flabelliformis</i>	Fantail Cuckoo		/	1/1	1/	4/2
Tytonidae						
<i>Tyto alba</i>	Barn Owl		-/1	-/-	/	/1
<i>Tyto multipunctata</i>	Lesser Sooty Owl		-/-	-/-	-/-	1/2
Strigidae						
<i>Ninox connivens</i>	Barking Owl		-/-	-/1	-/-	-/1
<i>Ninox boobook</i>	Boobook		2/2	-/1	-/-	-/1
Podargidae						
<i>Podargus papuensis</i>	Papuan Frogmouth		-/-	-/-	-/-	1/-
<i>Podargus strigoides</i>	Tawny Frogmouth		-/1	1/1	-/1	-/-
Aegothelidae						
<i>Aegothales cristatus</i>	Australian Owlet Nightjar		2/-	3/1	-/-	-/-
Caprimulgidae						
<i>Caprimulgus macrurus</i>	Large-tailed Nightjar		-/-	-/-	-/-	-/2
<i>Eurospododus mystacalis</i>	White-throated Nightjar		-/-	-/-	-/-	-/2
<i>Eurostodopus argus</i>	Spotted Nightjar		-/1	-/-	1/-	-/-
Alcedinidae						
<i>Ceyx azureus</i>	Azure Kingfisher		2/-	3/1	1/3	1/1
<i>Ceyx pusillus</i>	Little Kingfisher		-/-	1/1	-/-	-/1
<i>Dacelo leachii</i>	Blue-winged Kookaburra		1/-	-/3	1/3	-/-
<i>Dacelo novaeguineae</i>	Laughing Kookaburra		3/2	3/3	2/3	-/2

APPENDIX 1 cont.

SPECIES	COMMON NAME	A	B	C	D
<i>Melophaga notata</i>	Yellow-spotted Honeyeater	-/-	-/-	-/1	1/1
<i>Melophaga lewinii</i>	Lewins Honeyeater	-/-	-/-	-/-	4/3
<i>Meliphreptus albogularis</i>	White-throated Honeyeater	2/4	4/2	4/4	-/-
<i>Meliphreptus lunatus</i>	White-naped Honeyeater	-/-	-/-	-/-	-/1
<i>Myzomela obscura</i>	Dusky Honeyeater	-/-	-/1	-/1	-/3
<i>Myzomela sanguinolenta</i>	Scarlet Honeyeater	/1	-/1	1/1	/3
<i>Philemon argenteiceps</i>	Silver-crowned Friarbird	1/-	-/-	-/-	-/-
<i>Philemon citreogularis</i>	Little Friarbird	-/4	-/3	-/-	-/-
<i>Philemon corniculatus</i>	Noisy Friarbird	-/4	-/3	-/3	-/-
<i>Ramsayornis modestus</i>	Brown-backed Honeyeater	-/-	-/-	-/2	-/-
<i>Xanthotis macleayana</i>	Macleay's Honeyeater	-/-	-/-	-/-	2/2
Estrildidae					
<i>Lonchura punctulata</i>	Spice Finch	-/-	1/-	-/-	-/-
<i>Neochmia temporalis</i>	Red-browed Finch	/	/	3/3	1/
<i>Taeniopygia bichenovii</i>	Double-barred Finch	1/-	-/-	-/-	-/-
Oriolidae					
<i>Oriolus sagittatus</i>	Olive-backed Oriole	-/1	1/-	-/-	3/1
Dicuridae					
<i>Dicurus bracteatus</i>	Spangled Drongo	-/-	-/1	1/-	-/1
Grallinidae					
<i>Grallina cyanoleuca</i>	Peewee	3/4	4/3	2/3	/
Corcoracidae					
<i>Corcorax melanorhamphos</i>	White-winged Chough	-/-	2/1	1/2	-/-
<i>Struthidea cinerea</i>	Apostlebird	4/2	2/2	-/1	-/-
Artamidae					
<i>Artamus leucorhynchus</i>	White-breasted Woodswallow	-/-	-/1	-/-	1/1
Cracticidae					
<i>Cracticus nigrogularis</i>	Pied Butcherbird	2/3	4/4	1/2	-/-
<i>Cracticus torquatus</i>	Grey Butcherbird	3/3	3/3	1/2	-/-
<i>Gymnorhina tibicen</i>	Australian Magpie	4/4	4/4	3/4	-/-
<i>Strepera graculina</i>	Pied Currawong	1/1	1/1	3/3	2/2
Ptilonorhynchidae					
<i>Ailuroedus melanotis</i>	Spotted Catbird	-/-	-/-	-/-	1/-
<i>Chlamydera nuchalis</i>	Great Bowerbird	3/1	1/-	-/1	-/-
<i>Ptilonorhynchus violaceus</i>	Satin Bowerbird	-/-	-/-	-/-	1/-
Paradisaeidae					
<i>Ptiloris victoriae</i>	Victoria's Riflebird	/	-/-	/	3/3
Corvidae					

SPECIES	COMMON NAME	A	B	C	D
<i>Rhipidura rufifrons</i>	Rufous Fantail	/	-/-	-/-	1/3
Eopsaltridae					
<i>Eopsaltria australis</i>	Eastern Yellow Robin	-/-	-/-	-/1	4/3
<i>Heteromyias cinereifrons</i>	Grey-headed Robin	-/-	-/-	-/-	1/1
<i>Microeca flavigaster</i>	Lemon-breasted flycatcher	-/-	-/-	-/3	-/-
<i>Microeca leucophaea</i>	Jacky Winter	2/-	/	/	-/-
<i>Tregellasia capito</i>	Pale-yellow Robin	/	-/-	/	2/3
Pachycephalidae					
<i>Colluricincla boweri</i>	Bowers Shrike-Thrush	-/-	-/-	/	1/-
<i>Colluricincla harmonica</i>	Grey Shrike-Thrush	/	/	-/-	2/1
<i>Colluricincla megarrhyncha</i>	Rufous Shrike-Thrush	/	/	/	4/4
<i>Pachycephala pectoralis</i>	Golden Whistler	/	-/-	-/-	4/3
<i>Pachycephala rufiventris</i>	Rufous Whistler	2/4	1/2	4/4	1/1
Neosittidae					
<i>Daphoenositta chrysoptera</i>	Sittella	-/-	-/-	-/-	1/-
Climacteridae					
<i>Climacteris picumnus</i>	Brown Treecreeper	/	1/-	-/-	-/-
<i>Cormobates leucophaea</i>	White-throated Treecreeper	/	-/-	/	4/3
Dicaeidae					
<i>Dicaeum hurdinaceum</i>	Mistletoebird	/1	-/-	-/-	3/1
Pardalotidae					
<i>Pardalotus punctatus</i>	Spotted Pardalote	/	/	-/-	2/1
<i>Pardalotus striatus</i>	Striated Pardalote	4/4	4/4	4/3	2/-
Zosteropidae					
<i>Zosterops lateralis</i>	Silveryeye	-/-	-/-	-/-	3/3
Meliphagidae					
<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	-/-	-/-	-/-	-/1
<i>Cissomela pectoralis</i>	Banded Honeyeater	-/-	-/-	-/2	-/-
<i>Entomyzon cyanotis</i>	Blue-faced Honeyeater	4/4	3/3	2/2	-/-
<i>Meliphaga chrysops</i>	Yellow-faced Honeyeater	/	/	-/-	1/3
<i>Meliphaga flavescens</i>	Yellow-tinted honeyeater	/	-/-	-/-	-/-
<i>Meliphaga flava</i>	Yellow Honeyeater	/	/	1/-	/
<i>Meliphaga frenata</i>	Bridled Honeyeater	/	-/-	/	-/1
<i>Meliphaga fusca</i>	Fuscous honeyeater	-/-	-/-	-/-	-/-
<i>Lichmera indistincta</i>	Brown Honeyeater	-/-	-/1	1/3	1/2
<i>Manorina flavigula</i>	White-rumped Miner	2/4	4/3	-/-	-/-
<i>Manorina melanocephala</i>	Noisy Miner	2/3	2/4	-/3	-/-

APPENDIX 1 cont.

SPECIES	COMMON NAME		A	B	C	D
<i>Corvus coronoides</i>	Australian Raven		-/3	-/-	-/-	-/-
<i>Corvus orru</i>	Australian Crow		4/3	4/3	3/3	-/2

Part 3. Reptiles of the study area. The index of abundance is based on the following criteria : (-) not recorded at this site; 1 - observed once during the field trip; 2 - observed several times; 3 - common, observed most days; 4 - abundant, observed a number of times every day, usually at several locations. For further explanation see Part 1. Species names follow Ingram & Raven (1991).

SPECIES	COMMON NAME		A	B	C	D	E
Gekkonidae							
<i>Diplodactylus steindachneri</i>		HP	1/1	-/-	-/-	-/-	HP
<i>Gehyra dubia</i>		H	-/1	2/1	1/1	-/-	-
<i>Heteronotia binoei</i>	Bynoe's Gecko	H	3/3	-/2	2/2	-/-	-
<i>Oedura castlenau</i>	Northern Velvet Gecko	H	-/-	2/2	-/-	-/-	-
Scincidae							
<i>Carlia rostralis</i>		H	-/-	/	-/-	/	1
<i>Carlia jamouli</i>		H	-/-	/	/1	/1	1
<i>Carlia munda</i>	HP	1/1	/	2/2	-/-	-	-
<i>Carlia mundivensis</i>		H	-/1	-/-	2/2	-/-	-
<i>Carlia rubigularis</i>		H	-/-	-/-	-/-	3/3	-
<i>Cryptoblepharus virgatus</i>		H	3/-	2/2	2/2	-/-	2
<i>Ctenotus spaldingi</i>		H	-/-	/	-/-	-/1	-
<i>Egernia striolata</i>	Tree Skink	H	-/-	1/-	-/-	-/-	-
<i>Sphenomorphus quoyii</i>	Water Skink	SH	-/-	-/-	-/-	1/2	-
<i>Lampropholis basiliscus</i>		H	-/-	-/-	-/-	1/1	-
<i>Lygisaurus foliorum</i>		H	-/-	-/-	-/-	-/1	-
<i>Menetia greyii</i>		HP	1/1	-/-	-/-	-/-	-
<i>Morethia taeniopleura</i>	Fire-tailed Skink	HP	3/1	-/-	3/2	-/-	-
Agamidae							
<i>Pogona barbata</i>	Bearded Dragon	HS	-/-	1/1	-/-	-/-	-
<i>Diporiphora australis</i>	Two-line Dragon	HS	-/-	/	1/1	-/-	-
<i>Physignathus lesueuri</i>	Water Dragon	HS	-/-	-/-	-/-	2/1	1
Varanidae							
<i>Varanus scalaris</i>	Spotted Tree-monitor	H	1/-	-/-	-/-	-/2	-
<i>Varanus varius</i>	Lace Monitor	H	-/-	-/-	-/1	-/1	1
Boidae							
<i>Aspidites melanocephalus</i>	Black-headed Python	H	1/-	-/-	-/-	-/—	-
<i>Morelia amethystina</i>	Amethystine Python	H	/	-/-	-/-	1/-	-
<i>Morelia maculosa</i>	Childrens Python	HS	2/-	-/-	/	/	-
Colubridae							
<i>Tropidonophis mairii</i>	Keelback	H	-/-	-/-	-/1	-/-	1
<i>Dendrelaphis punctulata</i>	Common Tree Snake	H	-/-	-/-	-/-	1/22	-

Elapidae							
<i>Demansia vestigiata</i>	Black Whipsnake	S	-/-	-/-	1/-	-/-	-
<i>Demansia psammophis</i>	Yellow-faced Whipsnake	H	-/-	-/-	-/-	1/22	-
<i>Furina ornata</i>	Orange-naped Snake	H	-/1	-/-	-/-	-/-	-
<i>Pseudechis porphyriacus</i>	Red-bellied Black Snake	SH	-/-	-/-	/	3/3	-
<i>Pseudonaja textilis</i>	Eastern Brown Snake	HS	2/-	-/-	-/-	-/1	-
<i>Rhinoplocephalus nigriscens</i>	Small-eyed Snake	H	/	-/-	-/-	-/1	-
Chelidae							
<i>Elseya latisternum</i>	Sawshell Tortoise	H	-/-	1/2	2/2	-/-	-
<i>Emydura kreffii</i>	Kreff's River Tortoise	H	-/-	1/2	1/1	-/-	-

Part 4. Frogs of the study area. Species names follow Ingram & Raven (1991). For further explanation see Part 1.

SPECIES	COMMON NAME		A	B	C	D
Bufonidae						
<i>Bufo marinus</i>	Cane Toad	HSP	4/4	4/4	4/4	4/4
Hylidae						
<i>Cyclorana novaezealandiae</i>		H	2/-	-/-	-/-	-/-
<i>Litoria alboguttata</i>	Green-stripe Frog	H	2/-	-/-	-/-	-/-
<i>Litoria caerulea</i>	Green Tree Frog	HSP	2/-	1/-	1/-	1/-
<i>Litoria inermis</i>		HS	3/3	3/3	1/1	/
<i>Litoria latopalmata</i>		H	-/-	-/-	-/2	-/-
<i>Litoria leseuri</i>	Stony-creek Frog	HSP	-/-	3/3	3/3	3/3
<i>Litoria nasuta</i>	Striped Rocket Frog	HS	/	-/2	2/	3/3
<i>Litoria rothii</i>	Red-eyed Tree Frog	H	1/1	1/-	/	/
<i>Litoria rubella</i>	Naked Tree Frog	PH	3/-	-/-	-/-	-/-
Myobatrachidae						
<i>Limnodynastes ornatus</i>	Ornate Burrowing Frog	PHS	4/2	1/1	2/-	-/—
<i>Limnodynastes peronii</i>	Striped Marshfrog	H	-/-	-/2	-/-	-/2
<i>Limnodynastes tasmaniensis</i>	Spotted Marshfrog	H	-/-	-/-	1/-	-/-
<i>Uperoleia lithomoda/mimula</i>		PH	3/-	-/-	-/-	-/-

APPENDIX 1 cont.

Part 5. Fish of the study area. An abundance index indicates the number of individuals caught per sample as follows: -, not observed at this site; 1, observed at least once during each sampling period; 2, observed several times during sampling period; 3, observed regularly and caught in most seine sweeps; 4, caught in every seine sweep usually in large numbers. Species names follow Allen (1989). "Burd" and "Pus" refer to species recorded by other workers (see text). No samples taken at sites 7, 8 & 9 in second trip. Catchments are S, Star; K, Keelbottom; F, Fanning; and R, Reid.

	1	2	3	4	5	6	7	8	9	10	11	Burd	Pus
Catchment: S	S	S	S	K	K	R	F	F	S	K			F&K
Family Anguillidae													
<i>Anguilla reinhardtii</i> (Eel)	-	1/-	1/-	1/-	1/-	1/-	1/-	-	1/-	-	-	Y	-
Family Clupeidae													
<i>Nematolosa erebi</i> (Bony bream)	-1	-1	4/1	3/1	-1	3/3	-1	3/-	-1	-	-	Y	Y
Family Ariidae													
<i>Arius graeffei</i> (Salmon catfish)	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	Y	
Family Plotosidae													
<i>Neosilurus hyrtlai</i> (Hyrtl's tandan)	-1	1/-	-1	-1	-1	-1	-1	2/-	-1	-1	-1	Y	Y*
Family Belontiidae													
<i>Strongylura krefftii</i> (Freshwater longtom)	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	Y	-
Family Melanotaeniidae													
<i>Melanotaenia s. splendida</i> (Australian rainbow fish)	4/4	4/4	4/4	4/4	4/4	4/4	2/-	4/-	4/-	-	-	Y	Y
Family Atherinidae													
<i>Craterocephalus stercusmuscarum</i> (Fly-specked hardihead)	4	-4	3/2	1/4	-1	-1	-1	-1	-1	-1	-1	-	Y
Family Ambassidae													
<i>Ambassis agassizi</i> (Agassiz's glassfish)	-1	2/-	1/-	1/2	1/-	1/4	1/-	1/-	3/-	1/-	1/-	-	Y
Family Teraponidae													
<i>Leiopotherapon unicolor</i> (Spangled perch)	-1	2/3	2/3	2/-	2/3	3/4	1/-	1/-	1/-	1/-	-1	Y	Y
<i>Amniataba percooides</i> (Barred grunter)	-2	2/3	2/3	-1	2/-	2/-	1/-	1/-	1/-	1/-	1/-	Y	Y
<i>Hephaestus fuliginosus</i> (Sooty grunter)	2/2	2/2	-1	-	-1	-1	2/-	1/-	1/-	1/-	1/-	Y	Y
<i>Scortum parviceps</i> (Small-headed grunter)	-1	-1		1/-	1/-	1/-	-1	-1	-1	-1	-1	1/-	Y
Family Apogonidae													
<i>Glossamia aprion</i> (Mouth almighty)	-1	-1	-1	1/-	1/-	1/-	1/-	1/-	1/-	1/-	-1	Y	-
Family Toxotidae													
<i>Toxotes chatareus</i> (Seven-spot archerfish)	-1	-1	1/-	1/-	-1	-1	-1	1/-	1/-	1/-	1/-	Y	Y
Family Eleotridae													
<i>Mogurnda adspersa</i> (Purple-spotted gudgeon)	2/2	2/2	3/2	2/2	2/2	2/3	-1	-1	2/-	2/-	-1	-	Y
<i>?Hypseleotris compressa</i> (Empire gudgeon)	1/-		1/-		1/-	1/-	1/-	1/2	1/-	1/-	4/-	-1	-1
<i>Philypnodon grandiceps</i> (Flathead gudgeon)	-1	-1	-1	1/-	-1	-1	1/-	1/-	1/-	1/-	1/-	Y	
Family Gobiidae													
<i>Glossogobius ?giurus</i> (Flathead goby)	-1	-1	1/-	1/-	1/-	1/-	1/-	-1	1/-	-1	-1	Y	

VERTEBRATE FAUNA OF THREE MOUNTAIN TOPS IN THE TOWNSVILLE REGION, NORTH QUEENSLAND: MOUNT CLEVELAND, MOUNT ELLIOT AND MOUNT HALIFAX

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Vertebrate fauna surveys were carried out on the summits of Mount Cleveland, Mount Elliot and Mount Halifax in north Queensland. The main focus was on mammals and birds, but observations on all vertebrate groups are included. Habitats included rainforest and open eucalypt/casuarina forest. The surveys recorded a total of 136 species of vertebrates including 17 mammal, 77 bird, 32 reptile and 10 frog species. Habitat descriptions and measures of relative abundance for mammals and birds are included. □ *Survey, vertebrate, mountain, north, Queensland, Australia.*

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This paper reports the findings of vertebrate fauna surveys conducted on three mountain tops in the Townsville region of north Queensland. Most of the effort of the survey was directed at mammal and bird communities. However, all vertebrates were recorded and the data are included here. Reptiles, amphibians and invertebrates are dealt with in detail by Graham (1991). The fauna surveys were part of multidisciplinary fieldwork examining the suitability of Mount Elliot, Mount Cleveland and Mount Halifax for the placement of a radar tower by the Civil Aviation Authority.

Mountain top habitats are usually restricted and isolated from other patches of similar habitat. As well, there are usually endemic species associated with these restricted areas of habitat and, because endemic species were of special concern, fieldwork was mostly concentrated on the summit and the high ridges and saddles of the mountains.

The primary aim of the surveys was to provide a baseline description of the fauna of these mountain tops. Therefore, sampling was designed to record the presence of as many species as possible. This was achieved by using a variety of techniques in as many different micro-habitats (or habitat patches) as possible. Intensive sampling was conducted in each patch of different habitat within each study area. Selection of specific sub-sites was primarily based on vegetation, topography and substrate types. The vegetation classifications used were those of Walker & Hopkins (1990). Each mountain was sampled twice, during the early wet season (December 1990) and again in the early dry season (April 1991).

Previous mammal and bird surveys were carried out in the area by Lavery (1968) (birds), Lavery & Johnson (1968) (mammals), Lavery & Johnson (1974) (mammals) and Lavery & Seton (1974) (birds).

SITE DESCRIPTIONS

MOUNT CLEVELAND

Mount Cleveland (19°20'S, 147°03'E) is situated within Bowling Green Bay National Park, approximately 25km east of Townsville (Fig. 1). At 558m it is substantially lower than other mountains in the vicinity. Average annual rainfall is approximately 1000mm most of which occurs during the months December to March.

The vegetation at the summit of Mount Cleveland primarily consists of a relatively dense tree layer of *Allocasuarina torulosa* and mixed eucalypts, a dense middle layer of *Xanthorrhoea johnsonii* and a ground layer dominated by Blady Grass (*Imperata cylindrica*), over a rocky substrate.

Sub-sites selected for intensive sampling on Mount Cleveland were (topographic map used was Bowling Green 1:50 000, Sheet 8359-111, Edition 1-AAS, Series R 733):

C1 Mount Cleveland summit (Grid ref. 030706, altitude 558m): Mammal traps were laid in a circle around the summit ridge. The terrain was steep with large boulders and rock overhangs. Vegetation classification: very tall *Xanthorrhoea* shrubland above tall grassland (X4V/G3M). There was also dense vegetation, including some

rainforest taxa, in the gaps between the large boulders.

C2 Saddle between camp and summit (Grid ref. 033708, altitude 480m): the saddle was mostly flat with relatively few rocky outcrops. Vegetation classification: *Allocasuarina torulosa* dominated mid-high open forest with sclerophyll emergents over a very tall *Xanthorrhoea johnsonii* dominated shrubland (ALTOR ET6M/X4S). There were also patches of dense Blady Grass (*Imperata cylindrica*) in the more open areas.

C3 Rainforest (Grid ref. 034706, altitude 460m): Rainforest (c.2ha) was present in the catchment area of several rocky gullies just to the south of site C2. Vegetation classification: simple notophyll mixed tall closed forest (T7D S5M6).

C4 Rocky ridge (Grid ref. 036710, altitude 470m): The area was very rocky with outcrops of large granite boulders. The vegetation here is classified the same as site C2 (ALTOR ET6M/X4S), but it was much more rocky, the *Xanthorrhoea* was not as dense, and there were no significant areas of Blady Grass.

MOUNT ELLIOT

Mount Elliot (19°30'S, 146°57'E) is situated approximately 30km south-east of Townsville (Fig. 1) and, with an elevation of 1221m, is the highest mountain in the Townsville region. The group of mountains associated with Mount Elliot runs almost due north-south and hence they are influenced by the southeasterly trade-winds which blow up the Queensland coast. The area receives approximately 1200mm of rainfall annually, although the mountain top could be expected to receive considerably more than this due to its greater elevation. The majority of rainfall occurs during the months December to March.

Mount Elliot is entirely within Bowling Green Bay National Park and appears on the register of the National Estate. Unlike most areas to the north, Mount Elliot appears not to have been logged and, hence, remains relatively undisturbed. The rainforest on Mount Elliot is not contiguous with the northern forest and represents an island of forest surrounded by dry open woodland.

Sub-sites selected for intensive sampling on Mount Elliot were (topographic map used was Mount Elliot (Special), Edition 1, Series R733, 1:50 000.):

E1 (Grid ref. 109582, Altitude 1200m): narrow, steep summit ridge with Simple notophyll tall mixed closed forest with *Archontophoenix alexandrae*



FIG.1. Map of Townsville region showing the locations of the study sites.

emergents (AT7D S5M6). This area was typical of the summit with a rocky substrate and a well developed understorey vegetation.

E2 (Grid ref. 109581, Altitude 1200m): ridge top clearing, classified as Dwarf closed vineland with *Archontophoenix alexandrae* and *Cyathea* sp. emergents (AL4D). This site was representative of a number of similar clearings near to the summit of Mount Elliot, with a very dense ground cover of vines and scramblers about 1m thick. There is virtually no canopy except an occasional palm.

E3 (Grid ref. 112576, Altitude 1150m): wide ridge top with Simple notophyll mixed very tall closed forest (T8D S5M2). The vegetation at this site has a more open understorey than site E1.

E4 (Grid ref. 114574, Altitude 1150m): headwaters of eastern catchment area. The forest here was taller with fewer small saplings and a distinctive middle layer of the tree fern *Cyathea rebecca*. Classification was Simple notophyll mixed very tall closed fern forest (T8D S5M2).

MOUNT HALIFAX

Mount Halifax (19°07'S, 146°22'E), situated 50km west north-west of Townsville (Fig. 1), is the highest mountain, at 1064m, in the Paluma Range. It is a very wet area and the average annual rainfall for the region is approximately 2600mm, with the majority falling during the period December to March.

Sub-sites selected for intensive sampling were (Map used was Rollingsstone, Series R733, Sheet 8159 1, Edition 3-AAS 1:50 000):

H1 (Grid ref. 341862, Altitude 1020m): wet, ridge-top rainforest (very wet due to almost continuous cloud drip) - the SE ridge from the summit.

Vegetation Classification: Simple Notophyll Mixed Tall Closed Forest T7D S5M6.

H2 (Grid ref. 340863, Altitude 1040m): drier rainforest on the western slope of the SE ridge. Vegetation classification: T7D S5M6.

H3 (Grid ref. 344861, Altitude 1020m): taller rainforest on narrow ridge and saddle SE of camp. Vegetation classification: Simple Notophyll Mixed Very Tall Closed Forest T8D S5M6.

H4 (Grid ref. 342862, Altitude 1040m): heath vegetation near summit ridge. Vegetation classification: mid-high *Leptospermum amboinense* Open Forest above a tall sparse heathland and mid-high closed formland LEAMB T6M/Z4V/F2D.

H5 (Grid ref. 339864, Altitude 1060m): dense, low sclerophyllous vegetation on summit. Vegetation classification: Dwarf *Cullistemon viminalis* closed forest with sclerophyll emergents above a mid-high closed formland (ET4D/F2D).

METHODS

IDENTIFICATION

Voucher specimens of mammals, reptiles and amphibians that were difficult to identify were collected and lodged with the Queensland Museum (mammals) or with Queensland National Parks and Wildlife Service (reptiles and amphibians). Catalogue numbers are as yet unavailable as not all of the material has been sorted. Species worthy of special mention here are those bird observations which are range extensions (Victoria Riflebird, *Ptiloris victoriae*, Grey-Headed Robin, *Heteromyias cinereifrons*, Bridled Honeyeater, *Meliphaga frenata*, and Bower's Shrike-Thrush, *Colluricincla boweri*), and the small mammals *Rattus fuscipes* and *Melomys cervinipes*. No voucher specimens of birds were taken. Observations of Grey-Headed Robins and Bridled Honeyeaters were numerous and reliable, however only one sighting was made of Victoria's Riflebird and Bower's Shrike-thrush. *Rattus fuscipes* is very similar to *R. leucopus*. However, several skulls were examined from Mount Halifax and Mount Elliot and these proved to be *R. fuscipes*. In addition, two adult females on Mount Elliot had eight nipples (*R. fuscipes* has eight nipples while *R. leucopus* has six). As well, several specimens of *Melomys cervinipes* were identified on the basis of molar dentition and in the field on weight, fur texture and fur colour. The average weight of *M. cervinipes* on Mount Cleveland was 85g with an adult range of 70-115g. This differs from the range of 45-65g for *M. burtoni* (Strahan, 1983). Obviously these identifications

do not preclude the possibility of either *Rattus leucopus* or *Melomys burtoni* being present. Also there is considerable evidence showing that in north Queensland *M. cervinipes* is a forest generalist rather than a closed forest specialist and has much broader habitat preferences than previously thought (Winter et al., 1984; Williams, unpub. data).

MAMMAL TRAPPING

All of the sub-sites were trapped for four consecutive nights on each trip. Sub-sites C1, C2, C3 and C4 (Mount Cleveland) and sub-sites E1, E2, E3 and E4 (Mount Elliot) all had 25 Elliot "type A" traps and five wire cage "handicoot" traps. Sub-sites H1, H2 and H3 (Mount Halifax) had 20 Elliot traps, while sub-site H4 and H5 had 10 Elliot traps and two cage traps. Traps were placed at 10m intervals with cage traps equally spaced along the transect. Traps were baited with a mixture of rolled oats, peanut butter and vanilla essence. Cage traps were also baited with sardines to attract carnivores (e.g. quolls). Two drift fence/pit trap lines were set up at Mount Elliot and Mount Halifax. Each drift fence consisted of 50m of fence (30cm high) with six pit traps (20 litre plastic drums) at about 7m intervals.

Data collected from trapped animals included species, sex, reproductive status and weight. Each animal was marked with a small notch in the right ear and then released.

BIRD OBSERVATIONS

A walking transect (c.20min) was conducted at each sub-site for four consecutive mornings (in conjunction with clearing the mammal trap lines). An additional afternoon search (c.2hr) was conducted at each sub-site. This search included observations of birds, reptiles and amphibians. Three dawn choruses (1hr) per trip were also conducted at each mountain. All incidental bird observations were also recorded. Due to the high mobility of birds and the relatively short distance between sub-sites the avifauna was not separated into the different sub-sites for each mountain.

WALKING TRANSECTS

Night

Spotlighting transects of 1-1.5hr were conducted in each of the sub-sites on each mountain on both trips for mammals, birds, reptiles and amphibians. Two spotlights (30w) were used in each survey.

Day

Daylight walking transects of c. 2hr were con-

ducted each day (once at each sub-site) to search for birds and reptiles.

RESULTS

Mount Halifax had the highest diversity of birds (55 species) (Table 1) and ground-dwelling mammals (seven species) with Mount Cleveland having the greatest diversity of reptiles (18 species). Mount Elliot was notable in that it had the lowest observed diversity of all groups (Table 1).

The diversity of terrestrial vertebrates observed during these surveys is summarised in Table 1 and a complete species list with an index of relative abundance for each species (mammals and birds) is given in Appendix 1. Detailed mammal trapping results for each sub-site are included in Appendix 2.

MT CLEVELAND

There were considerable differences between the small mammal assemblages of each sub-site on the upper ridges of Mount Cleveland (appendix 2):

- (1) The summit (site C1) and the rocky ridge (site C4) supported a small mammal assemblage consisting of *Dasyurus hallucatus*, *Melomys cervinipes*, *Isodon macrurus*, and *Petrogale inornata*. Neither *D. hallucatus* or *P. inornata* were observed at the other sites. This is not surprising given the preference of these species for rocky habitat.
- (2) Site C2 was dominated by *Melomys cervinipes*. Its density was very high at this site (20 individuals) with new individuals still being trapped after four days. The high density of *Xanthorrhoea* could be one of the factors contributing to this because several individuals of *M. cervinipes* were observed nesting within the head of the grass trees and also eating the seeds. No *D. hallucatus* or *P. inornata* were observed in this habitat.
- (3) The rainforest (site C3) contained fewer *Melomys cervinipes* in comparison to the other sites. This area may be more important during the dry season when water is not readily available in the drier areas.

Forty-three species of birds were observed on Mount Cleveland (Appendix 1). There was a much higher level of bird activity in, and on the edge, of the rainforest than elsewhere on the mountain. Generally the bird community was typical of the open forest of the Townsville region. However, due to the presence of the rainforest patch, there were also a number of closed forest species present (e.g. Scrub Turkey, Purple-

crowned Pigeon, Wompoo Pigeon, Noisy Pitta, and Bower's Shrike-thrush).

MT HALIFAX

The summit area of Mount Halifax was found to have a mammal community typical of rainforest in this region (Appendix 1 and 2). The rainforest small mammal community was dominated by *Rattus fuscipes* and the small patches of heath vegetation were dominated by *Melomys cervinipes*.

There were several species which were expected but were not observed during the field surveys. These include the Red-legged Pademelon (*Thylogale stigmatica*), Brushtail Possum (*Trichosurus vulpecula*) and Green Ringtail (*Pseudochirops archeri*).

There were several small areas of heath that were of local significance (summit - grid ref. 339864 and near campsite - grid ref. 342862). The heath represented a very different habitat from the surrounding rainforest and, as such, significantly increased the habitat diversity of the area. Although the areas were probably too small to support vertebrates unique to that habitat, such as mammals and birds, there was a significantly different small mammal community present (compare sites H4 & H5 to sites H1, H2 & H3 in Appendix 2). It is also highly likely that these patches of heath would support restricted and endemic invertebrates (Graham, 1991). The heath contained concentrations of myrtaceous plant species such as *Leptospermum amboinense* and *Callistemon* sp., which could be an important seasonal food source for nectivorous birds and mammals.

MT ELLIOT

The results of the mammal trapping indicate that the Mount Elliot rainforest has a relatively depauperate small mammal community (Appendices 1 and 2). Only two species, *Rattus fuscipes* and *Melomys cervinipes* were trapped regularly and only in low numbers (Appendix 2). A single *Planigale maculata* was caught in an insect formalin trap. No sampling was conducted in the open forest; however this area was sampled by Lavery & Johnson (1974).

DISCUSSION

The three mountains examined differ considerably in topography and vegetation. These differences are reflected in relative abundances and species diversities of mammals and birds. Gra-

TABLE 1. Diversity of vertebrates by taxonomic group for Mount Cleveland, Mount Halifax and Mount Elliot

VERTEBRATE GROUP	MOUNT CLEVELAND	MOUNT HALIFAX	MOUNT ELLIOT
MAMMALS			
Families	6	4	3
Species	9	7	5
BIRDS			
Families	20	24	16
Species	43	55	31
REPTILES			
Families	8	6	5
Species	18	10	7
AMPHIBIANS			
Families	2	3	3
Species	5	5	4
TOTALS			
Families	36	37	27
Species	75	77	45

ham (1991) has previously discussed the survey of reptiles and amphibians from this expedition. Mount Halifax had the most diverse vertebrate fauna overall, as might be expected from its position, which is contiguous with other mountains and comparable habitats in the Paluma range. Small patches of heath near the summit of Mount Halifax may increase the habitat heterogeneity enough to produce endemic arthropods (Monteith, pers. comm.), but the areas are probably too small to have a significant effect on vertebrate communities. Both Mount Cleveland and Mount Elliot are discrete mountains in which it may be expected that diversities would be lower due to smaller, more isolated summit habitats. The relatively high diversity at Mount Cleveland is probably due to high habitat heterogeneity on the summit ridges.

Mount Cleveland is an important part of Bowling Green Bay national park as the habitat on and near the summit is unique within the park and is not well represented elsewhere in the region. The habitat on the upper ridges (*A. torulosa*/*Xanthorrhoea* forest ALTOR ET6M/X4S) is not wide-

spread and contains a faunal community which is unusual (*Dasyurus hallucatus* and a high density of *Melomys cervinipes*). This community/habitat is therefore of significant importance to biological conservation both within this national park, and to the region. Patches of closed forest (e.g. site C3) are of great local significance as they greatly increase the diversity of habitats and the associated flora and fauna (as can be seen by the presence of a number of rainforest birds) although the much larger area of closed forest on nearby Mount Elliot is probably of greater regional significance.

The summit of Mount Elliot contains the largest block of rainforest within the Bowling Green national park and is regarded as being the southern limit of tropical rainforest proper (Winter & Atherton, 1987). The vertebrate fauna and flora surveys undertaken during this study also indicate that the rainforest on Mount Elliot has a high degree of affinity with the tropical rainforest to the north of Townsville. Taxa collected or noted by previous studies (Lavery 1968; Lavery & Johnson 1968; Lavery & Johnson 1974; Lavery & Seton, 1974) also indicate strong affinities with the rainforests along the Paluma Range to the north. There is one microhylid frog, *Cophixalus mcdonaldi*, endemic to the rainforest of Mount Elliot (Nix & Switzer, 1991; Zweifel, 1985). Very little is known about the biology of this very restricted species. *C. mcdonaldi* was calling during December and it appeared to be very common throughout the forest on the summit of Mount Elliot. Eight individuals were found during March by actively searching (three in rotted tree stumps, one in a crack between rocks, two under a flat rock and two sitting on a clutch of at least eight eggs inside a small (2cm diameter) hole in a solid rock face). Another interesting record was the capture of a *Planigale maculata* within rainforest when this species is usually considered to be an open forest species. It was unusual that no White-tailed Rats (*Uromys caudimaculatus*) were trapped or observed while spotlighting, since they have been recorded at Mount Elliot in the past, and are usually easy to trap and to spotlight.

Three species of birds recorded on Mount Elliot have not been recorded this far south before: Victoria's Riflebird, Bridled Honeyeater and Grey-headed Robin. These records increase the evidence of an affinity in the vertebrate fauna between the rainforest of Mount Elliot and tropical rainforest further to the north.

Mount Elliot is known to have a number of

endemic insect species, despite generally lower diversities than in the rainforests to the north (Graham, 1991). Mount Elliot is important in any biogeographical study of latitudinal trends in tropical biota, and greatly increases the local and regional biodiversity due to the inclusion of an area of tropical rainforest in an otherwise dry region.

COMMENTS ON TECHNIQUES

All sampling techniques have inherent biases that vary between taxa, seasons, habitats and weather conditions. Small mammals differ markedly in their relative trappability as illustrated by the capture of *Planigale maculata* in an insect formalin trap, which was not trapped in the small mammal traps. Pit traps (Mount Elliot, Mount Halifax) were found to be inefficient with respect to the effort required to install the pit lines. The pit traps were most useful in catching large ground dwelling invertebrates. Weather can have a large affect on observation biases with rain and/or mist making spotlighting and visual bird observations very difficult. Conversely, wet weather will increase the possibility of observing most amphibians and many reptiles. Most amphibians and reptiles are also less active during the winter months (dry season) making summer (wet season) sampling essential in tropical rainforests.

Habitat differences can have a drastic affect on the biases involved in most techniques. Dense vegetation makes visual observation of birds difficult and results in an increased importance of call identification. However, during these surveys it was found that, although most of the records were based on calls for the first two days, all bird species had been visually confirmed within five days. Dense vegetation also makes spotlighting for arboreal mammals very difficult, especially where there are no tracks or roads.

In summary, it is vital for vertebrate surveys to use as many different techniques as possible, and to sample during both wet and dry weather conditions to maximise the efficacy of the survey.

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APPENDIX 1

List of vertebrates observed during the fauna surveys of Mount Cleveland (Clv), Mount Hali-fax (Hal) and Mount Elliot (Ell). An index of abundance is given for mammals and birds for both the first and second field surveys (separated by a '/'). '-' — not observed, '0' — not ob-

served on this trip, '1' — uncommon/only seen once or twice, '2' — common/observed regularly, '3' — abundant/observed several times on every census, '*' — observed at least once at this site during the course of both surveys. Species names follow Ingram & Raven (1991).

SPECIES	COMMON NAME	Clv	Hal	Ell
MAMMALS				
<i>Dasyuridae</i>				
<i>Antechinus flavipes</i>	Yellow-footed Antechinus	-	2/2	
<i>Antechinus stuartii</i>	Brown Antechinus	-	1/1	-
<i>Dasyurus hallucatus</i>	Northern Quoll	2/0	-	-
<i>Planigale maculata</i>	Common Planigale	-	-	0/1
<i>Peramelidae</i>				
<i>Isodon macrourus</i>	Northern Brown Bandicoot	2/2		-
<i>Perameles nasuta</i>	Long-nosed Bandicoot		1/1	-
<i>Macropodidae</i>				
<i>Macropus agilis</i>	Agile Wallaby	1/1		
<i>Petrogale inornata</i>	Unadorned Rock Wallaby	1/1	-	-
<i>Pteropidae</i>				
<i>Nyctimene robinsoni</i>	Queensland Tube-nosed Bat	0/1		-
<i>Pteropus alecto</i>	Black Flying-fox	1/1	-	
<i>Syconycteris australis</i>	Queensland Blossom-bat	1/0	-	
<i>Muridae</i>				
<i>Melomys cervinipes</i>	Fawn-footed Melomys	3/3	3/3	2/2
<i>Mus musculus</i>	House Mouse	-		0/1
<i>Rattus fuscipes</i>	Bush Rat	-	3/3	3/2
<i>Uromys caudimaculatus</i>	White-tailed Rat	-	2/2	
<i>Suidae</i>				
<i>Sus scrofa</i>	Feral Pig	1/1	2/2	2/2
BIRDS				
<i>Casuariidae</i>				
<i>Casuaris casuaris</i>	Southern Cassowary	-	1/1	-
<i>Accipitridae</i>				
<i>Accipiter fasciatus</i>	Brown Goshawk	-	0/1	-
<i>Accipiter novaehollandiae</i>	Grey Goshawk	1/0	-	-
<i>Aquila audax</i>	Wedge-tailed Eagle	1/1	0/1	0/1
<i>Haliastur indus</i>	Brahminy Kite	0/1	-	-
<i>Falconidae</i>				
<i>Falco peregrinus</i>	Peregrine Falcon	-	1/0	-
<i>Megapodiidae</i>				
<i>Alectura lathami</i>	Brush Turkey	1/1	2/2	2/1
<i>Megapodius freycinet</i>	Scrubfowl	-	1/0	1/0
<i>Phasianidae</i>				
<i>Synoicus australis</i>	Brown Quail	0/1		
<i>Columbidae</i>				
<i>Chalcophaps indica</i>	Green-winged Pigeon	-	2/2	1/0
<i>Columba leucomela</i>	White-headed Pigeon	0/1	1/1	1/1

SPECIES	COMMON NAME	Clv	Hal	Ell
<i>Geopelia humeralis</i>	Bar-shouldered Dove	1/0		-
<i>Lopholaimus antarcticus</i>	Topknot Pigeon		1/0	1/0
<i>Macropygia amboinensis</i>	Brown Pigeon	-	2/1	2/1
<i>Ptilinopus magnificus</i>	Wompoo Pigeon	1/0	1/1	2/3
<i>Ptilinopus regina</i>	Red-crowned Pigeon	-	1/0	-
<i>Ptilinopus superbus</i>	Purple-crowned Pigeon	1/0	1/0	2/0
<i>Loridae</i>				
<i>Trichoglossus chlorolepidotus</i>	Scaly-breasted Lorikeet	-	0/1	-
<i>Cacatuidae</i>				
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo	1/1	2/2	0/1
<i>Psittacidae</i>				
<i>Alisterus scularis</i>	King Parrot	-	1/1	
<i>Platyercus elegans</i>	Crimson Rosella		2/3	-
<i>Cuculidae</i>				
<i>Centropus phasianinus</i>	Pheasant Coucal	3/3	-	-
<i>Chrysococcyx lucidus</i>	Shining Bronze-Cuckoo		1/1	-
<i>Cacomantis flabelliformis</i>	Fantail Cuckoo	-	0/2	0/3
<i>Tytonidae</i>				
<i>Tyto multipunctata</i>	Lesser Sooty Owl		0/1	
<i>Strigidae</i>				
<i>Ninox boobook</i>	Boobook Owl	1/1	-	1/0
<i>Podargidae</i>				
<i>Podargus strigoides</i>	Tawny Frogmouth	1/0	-	-
<i>Aegotheidae</i>				
<i>Aegotheles cristatus</i>	Australian Owlet Nightjar	1/0	—	
<i>Apodidae</i>				
<i>Apus pacificus</i>	Fork-tailed Swift	-	1/0	-
<i>Alcedinidae</i>				
<i>Dacelo leachii</i>	Blue-winged Kookaburra	0/1	-	-
<i>Dacelo novaeguineae</i>	Laughing Kookaburra	3/3	-	1/0
<i>Meropidae</i>				
<i>Merops ornatus</i>	Rainbow Bee-Eater	-	3/3	
<i>Pittidae</i>				
<i>Pitta versicolor</i>	Noisy Pitta	-	3/3	3/0
<i>Campephagidae</i>				
<i>Coracina lineata</i>	Barred Cuckoo-Shrike	-	1/0	-
<i>Coracina tenuirostris</i>	Cicadabird	0/1		-
<i>Lalage leucomela</i>	Varied Triller	2/2	-	-
<i>Orthonychidae</i>				
<i>Orthonyx spaldingii</i>	Northern Logrunner	-	3/3	
<i>Psophodes olivaceus</i>	Eastern Whipbird	-	3/3	-
<i>Maluridae</i>				

SPECIES	COMMON NAME	Clv	Hal	Ell
<i>Malurus elegans</i>	Red-backed Wren	1/0	-	-
Acanthizidae				
<i>Oreoscoptes gutturalis</i>	Fernwren	-	1/1	-
<i>Gerygone mouki</i>	Brown Warbler	-	0/2	0/1
<i>Gerygone palpebrosa</i>	Fairy Warbler	2/2	0/1	-
<i>Sericornis citreogularis</i>	Yellow-throated Scrubwren		1/1-	
<i>Sericornis frontalis</i>	White-browed Scrubwren	-	2/0	3/3
<i>Sericornis magnirostris</i>	Large-billed Scrubwren	-	1/2	0/2
Monarchidae				
<i>Monarcha melanopsis</i>	Black-faced Monarch	-	0/1	1/0
<i>Monarcha trivirgatus</i>	Spectacled Monarch	1/1	1/0	
<i>Myiagra cyanoleuca</i>	Satin Flycatcher	1/0		
<i>Myiagra rubecula</i>	Leaden Flycatcher	2/1		
<i>Rhipidura fuliginosa</i>	Grey Fantail	-	3/3	1/1
<i>Rhipidura rufifrons</i>	Rufous Fantail		1/1	
Eopsaltridae				
<i>Heteromyias cinereifrons</i>	Grey-headed Robin		3/3	3/3
<i>Tregellasia capito</i>	Pale-yellow Robin		3/3	2/3
Pachycephalidae				
<i>Colluricincla boweri</i>	Bowers Shrike-thrush	0/1	-	-
<i>Colluricincla megarrhyncha</i>	Rufous Shrike-thrush	3/3	1/1/1	
<i>Pachycephala pectoralis</i>	Golden Whistler		2/2	2/1
<i>Pachycephala rufiventris</i>	Rufous Whistler	-	1/0	-
<i>Pachycephala simplex</i>	Grey Whistler	-	1/0	1/0
Dicaeidae				
<i>Dicaeum hirundinaceum</i>	Mistletoebird	-	0/1	-
Meliphagidae				
<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill		2/3	1/0
<i>Meliphaga chrysops</i>	Yellow-faced Honeyeater	-		1/0
<i>Meliphaga frenatus</i>	Bridled Honeyeater	-	2/2	2/0
<i>Meliphaga gracilis</i>	Graceful Honeyeater	-	1/0	-
<i>Meliphaga notata</i>	Yellow-spotted Honeyeater	3/3	1/0	-
<i>Meliphaga lewinii</i>	Lewins Honeyeater	-	3/3	2/2
<i>Meliphaga lunatus</i>	White-naped Honeyeater	1/0	-	-
<i>Myzomela obscura</i>	Dusky Honeyeater	1/0	0/1	
<i>Philemon novaeguineae</i>	Helmeted Friarbird	1/0		
<i>Philemon corniculatus</i>	Noisy Friarbird	3/0	1/0	
<i>Phylidonyris nigra</i>	White-cheeked Honeyeater	-	0/1	
Estrildidae				
<i>Neochmia temporalis</i>	Red-browed Firetail	1/0	-	
Dicruridae				
<i>Dicrurus bracteatus</i>	Spangled Drongo	1/0		
Cracticidae				
<i>Sirepera graculina</i>	Pied Currawong	2/3	0/3	3/2
Ptilonorhynchidae				
<i>Ailuroedus melanotis</i>	Spotted Catbird		3/3	
<i>Scenopoetes dentirostris</i>	Toothbill Bowerbird	-	3/2	3/3
Paradisaeidae				
<i>Ptiloris victoriae</i>	Victoria's Riflebird	-	1/1	1/0

SPECIES	COMMON NAME	Clv	Hal	Ell
Corvidae				
<i>Corvus orru</i>	Australian Crow	2/0	-	
REPTILES				
Gekkonidae				
<i>Gehyra dubia</i>		*	-	*
<i>Heteronotia binoei</i>	Bynoe's Gecko	*	-	-
<i>Oedura ocellata</i>		*	-	-
<i>Oedura rhombifer</i>		*	-	-
Pygopodidae				
<i>Lialis burtonis</i>	Burton's Legless Lizard	*	-	-
Scincidae				
<i>Carlia pectoralis</i>		*		
<i>Carlia rhomboidalis</i>		*	-	-
<i>Carlia rubrigularis</i>		-	*	-
<i>Carlia schmeltzii</i>		*		
<i>Cyclodomorphus gerrardi</i>				*
<i>Egernia frerei</i>		*		
<i>Sphenomorphus quoyii</i>	Water Skink	-	*	-
<i>Lampropholis basiliscus</i>		-	*	*
<i>Lampropholis coggeri</i>		-	*	
<i>Lampropholis mirabilis</i>		-	-	*
<i>Sphenomorphus punctulatus</i>		*		-
Agamidae				
<i>Diporiphora australis</i>	Two-line Dragon	*		
<i>Physignathus lesueurii</i>	Water Dragon	-	*	-
Varanidae				
<i>Varanus scalaris</i>	Spotted Tree-monitor	*	*	-
<i>Varanus varius</i>	Lace Monitor	-	-	*
Boidae				
<i>Morelia amethystina</i>	Amethystine Python		*	-
<i>Morelia maculosa</i>	Childrens Python	*	-	-
<i>Morelia spilota</i>	Carpet Python	*	-	*
Colubridae				
<i>Dendrelaphis punctulata</i>	Common Tree Snake	*	*	-
Elapidae				
<i>Acanthophis antarcticus</i>	Death Adder	-	-	*
<i>Demansia vestigiata</i>	Black Whipsnake	*	-	-
<i>Demansia psammophis</i>	Yellow-faced Whipsnake	-	-	*
<i>Demansia torquata</i>	Collared Whipsnake	*	-	-
<i>Pseudechis porphyriacus</i>	Red-bellied Black Snake	-	*	-
<i>Pseudonaja textilis</i>	Eastern Brown Snake	*		
<i>Rhinoplocephalus nigrescens</i>	Snalleyed Snake		*	
AMPHIBIANS				
Bufo				
<i>Bufo marinus</i>	Cane Toad	*	*	*
Hylidae				
<i>Litoria caerulea</i>	Green Tree Frog	*	-	-
<i>Litoria fallax</i>		*	-	-
<i>Litoria gracilentia</i>		*	-	-

SPECIES	COMMON NAME	Civ	Hal	Ell
<i>Litoria leuseuri</i>	Stony-creek Frog	-	*	*
<i>Litoria nannotis</i>	Torrent Tree Frog	-	*	-
<i>Litoria rothii</i>	Red-eyed Tree Frog	*	-	-
Microhylidae				
<i>Cophixalus mcdonaldi</i>		-	-	*
<i>Cophixalus ornatus</i>		-	*	-
<i>Sphenophryne robusta</i>		-	*	-

APPENDIX 2

Results of small mammal trapping at each sub-site on Mount Cleveland, Mount Halifax and Mount Elliot. Data are the number of individuals caught per hundred trap nights at each trapping site. The results of each field trip (TRIP) are given separately.

MOUNT CLEVELAND					
SPECIES	TRIP	C1	C2	C3	C4
<i>Dasyurus hallucatus</i>	1	2.0	—	—	1.0
	2	—	—	—	—
<i>Isoodon macrourus</i>	1	2.0	2.0	1.0	2.0
	2	1.0	2.0	1.0	1.0
<i>Melomys cervinipes</i>	1	9.0	20.0	2.0	10.0
	2	19.0	23.0	6.0	21.0

MOUNT ELLIOT					
SPECIES	TRIP	E1	E2	E3	E4
<i>Melomys cervinipes</i>	1	1.1	3.2	2.2	—
	2	2.0	1.0	—	1.0
<i>Mus musculus</i>	1	—	—	—	—
	2	2.0	—	—	—
<i>Planigale maculata</i>	1	—	—	—	—
	2	—	—	1.0	—
<i>Rattus fuscipes</i>	1	4.3	2.2	4.3	5.4
	2	—	4.0	1.0	—

MOUNT HALIFAX						
SPECIES	TRIP	H1	H2	H3	H4	H5
<i>Antechinus flavipes</i>	1	3.8	—	2.5	2.5	—
	2	4.2	—	—	—	—
<i>Antechinus stuartii</i>	1	—	—	2.5	—	—
	2	2.1	—	—	—	—
<i>Melomys cervinipes</i>	1	1.3	—	—	5.0	10.0
	2	2.1	—	—	4.2	—
<i>Rattus fuscipes</i>	1	12.5	13.8	20.0	22.5	2.5
	2	16.7	14.6	18.8	8.3	29.2
<i>Uromys caudimaculatus</i>	1	2.5	1.3	1.3	—	—
	2	2.1	2.1	4.2	—	—



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